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Ecophysiological significance of nonhydraulic root-to-shoot signaling in control of stomatal behavior during soil drying

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Recommended Citation

Croker, Jennifer L., "Ecophysiological significance of nonhydraulic root-to-shoot signaling in control of stomatal behavior during soil drying. " Master's Thesis, University of Tennessee, 1997.
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To the Graduate Council:

I am submitting herewith a thesis written by Jennifer L. Croker entitled "Ecophysiological significance of nonhydraulic root-to-shoot signaling in control of stomatal behavior during soil drying." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Landscape Architecture.

Robert M. Augé, Major Professor

We have read this thesis and recommend its acceptance:

Tim Tschaplinski, Paul Hanson

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

ECOPHYSIOLOGICAL SIGNIFICANCE OF NONHYDRAULIC ROOT-TO-SHOOT SIGNALING IN CONTROL OF STOMATAL BEHAVIOR DURING SOIL DRYING

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jennifer L. Croker
August 1997

DEDICATION

I dedicate this thesis to my parents, brother and grandparents, Neil and Henrietta Croker, Brent Croker, and Henry and Margaret McElroy. Their love, support and encouragement have been invaluable throughout my education.

ACKNOWLEDGMENTS

I thank my major professor Dr. Robert M. Augé for all his endless help and advice, and for his friendship which made the whole degree process much more enjoyable. I thank my committee members, Dr. Tim Tschaplinski and Dr. Paul Hanson for their guidance. I thank the OHLD department heads, Dr. Douglas Crater, Dr. Don Williams and Dr. Mary Albrecht for the making it possible for me to attend graduate school. I am very grateful to Ann Stodola, Phil Flanagan, Mark Arena, Xiangrong Duan, and Dr. Willard Witte for their invaluable help with plant care, equipment use and many other things. I thank the office crew, Angie, Joy, Kathy and Nikki for their help and cheerful smiles. Finally, I wish to extend a big thanks to Millie Williams, Meg Rohs, Craig Green, Joel Keebler, Tammy Boss, Brendon Johnson, Clint Cagle, Mike Janis, Bob Inman, Jay Clark, Troy Ettel, Chris Kreh and all my other fellow graduate students for their friendship and sincere support for the past two years.

ABSTRACT

The objectives of this study were to: (1) characterize stomatal response of six deciduous tree species to nonhydraulic root-to-shoot signals of soil drying, and (2) test whether species sensitivity to nonhydraulic signaling is allied with their drought avoidance and tolerance profiles. Saplings of *Acer rubrum, Chionanthus virginicus, Cornus florida, Halesia carolina, Liriodendron tulipifera,* and *Oxydendrum arboreum* were grown with roots divided between two pots. Three treatments were compared: half of the root system watered and half droughted (WD), half of the root system watered and half severed (WS), and both halves watered (WW). Partial soil drying caused nonhydraulic declines in stomatal conductance (g_s) in all species, with maximum declines ranging from 31% to 57% of WS controls. Declines in stomatal conductance were closely related to declining soil matric potential at soil Ψ_m below -0.10 MPa. Soil Ψ_m required to cause declines in WD g_s to 80% of WS controls varied from -0.013 to -0.044 MPa. Stomatal conductance of some species declined and remained low as soil dried, while g_s of other species declined initially with declining soil moisture and then increased as soil dried further. Leaf osmotic potentials during soil drying were mostly similar among treatments. Stomatal responses were not correlated with previously identified lethal leaf water potentials or osmotic adjustment, suggesting that stomatal sensitivity to nonhydraulic root signals may not be mechanistically linked to other characteristics defining relative species drought tolerance.

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LIST OF ABBREVIATIONS

WW	fully-watered treatment
WD	half-dried treatment
WS	half-severed treatment
Ψ_π	osmotic potential
Ψ_m	soil matric potential
g_s	stomatal conductance
RWC	relative water content
Ψ	water potential

1. Introduction and Literature Review

Physiological drought resistance

Plants apparently use different strategies to survive in times of water stress (Ludlow et al. 1983). These strategies involve several mechanistically-linked physiological responses and morphological characteristics for dealing with drought (Ludlow 1989). Based on responses to water stress, plants can be generally classified as either drought avoiders or tolerators. Avoiders typically have tissues sensitive to dehydration that cannot survive prolonged periods of water stress. Avoidance strategy usually involves maximizing water uptake (e.g. deep roots) and/or reducing water loss (e.g. sensitive stomates to reduce transpirational water loss) (Ludlow 1989). Drought tolerators have tissues less sensitive to dehydration; thus they have few mechanisms to avoid dehydration and primarily use osmotic adjustment to endure drought (Ludlow et al.1983, Ludlow 1989). Most plants do not fit exactly into either strategy; rather there exists a continuum from extreme avoiders to extreme tolerators (Ludlow 1989).

Location of a particular plant on this continuum is determined primarily by the plant's sensitivity to dehydration (Ludlow 1989). The desiccation tolerance of plant tissue has been operationally defined as lethal leaf water potential (Ψ) or lethal leaf relative water content (RWC) (Ludlow 1989). These lethal leaf Ψ and RWC values are measured for the last living leaves of a plant during a continuous drying episode. Avoiders generally exhibit high lethal leaf Ψ and RWC while tolerators generally exhibit low lethal leaf Ψ and RWC. For example, cowpea (*Vigna unguiculata*), an extreme dehydration avoider, has a lethal leaf Ψ near -2 MPa (Bates and Hall 1981; Ebel et al. 1996). In comparison, three tropical grass species, determined to be dehydration tolerators, can withstand leaf Ψ as low as -12 MPa (Ludlow et al. 1985). Along with many herbaceous species, several woody species have been characterized according to their dehydration tolerance, including the six species examined in this study (e.g. Augé et al., unpublished; Bahari et al. 1985; Ni and Pallardy 1991; Pallardy and Rhodes 1993).

Characterizing the drought strategy of tree species in the forest ecosystem will be valuable in determining differences in productivity and survival during periods of reduced precipitation. Current research indicates that global climate change could result in reduced soil moisture among other effects. The dehydration tolerance of deciduous tree species influences their distribution (Hinckley et. al. 1981; Martin et al. 1987). Also, it is important to consider dehydration sensitivity and its impact on forest community structure during drought, particularly when studying the high rainfall area of the Southern Appalachians (Elliot and Swank 1994). A reduction in soil moisture could result in alterations in stomatal behavior and/or leaf growth; thus, understanding the drought strategy and the role of nonhydraulic signaling (discussed below) during periods of water stress will improve the accuracy of models predicting the impact of global climate change on forest community structure and species distribution. This research could also benefit the nursery and forestry industries economically in planning the best suited species for a given planting site.

Nonhydraulic, root-to-shoot signaling and stomatal behavior

The most sensitive indicator of a plant's overall physiological state is often stomatal behavior (Smith and Hollinger 1991). Stomata respond rapidly to changes in environmental conditions, including soil drying, allowing the plant to balance water loss with carbon uptake during periods of reduced soil moisture. Thus, studying how stomata respond to changes in amount of soil water is integral to understanding whole plant physiology during drought. Nonhydraulic, root-to-shoot signaling of soil drying is a relatively recent hypothesis concerning control of stomatal behavior. Previously, it was widely believed that soil drying led to a lower shoot water status which caused direct hydraulic limitation (Figure 1-1) of leaf growth and stomatal opening (Kramer 1983). However, reduced stomatal conductance (g_s) can occur in plants grown in drying soil in which shoot water status is held constant (Gollan et al. 1986). Thus, it appears that a nonhydraulic limitation (Figure 1-2) mechanism enables some plants to "sense" and respond to soil drying (Davies and Zhang 1991). This mechanism of sensing soil drying must logically originate in the roots and be

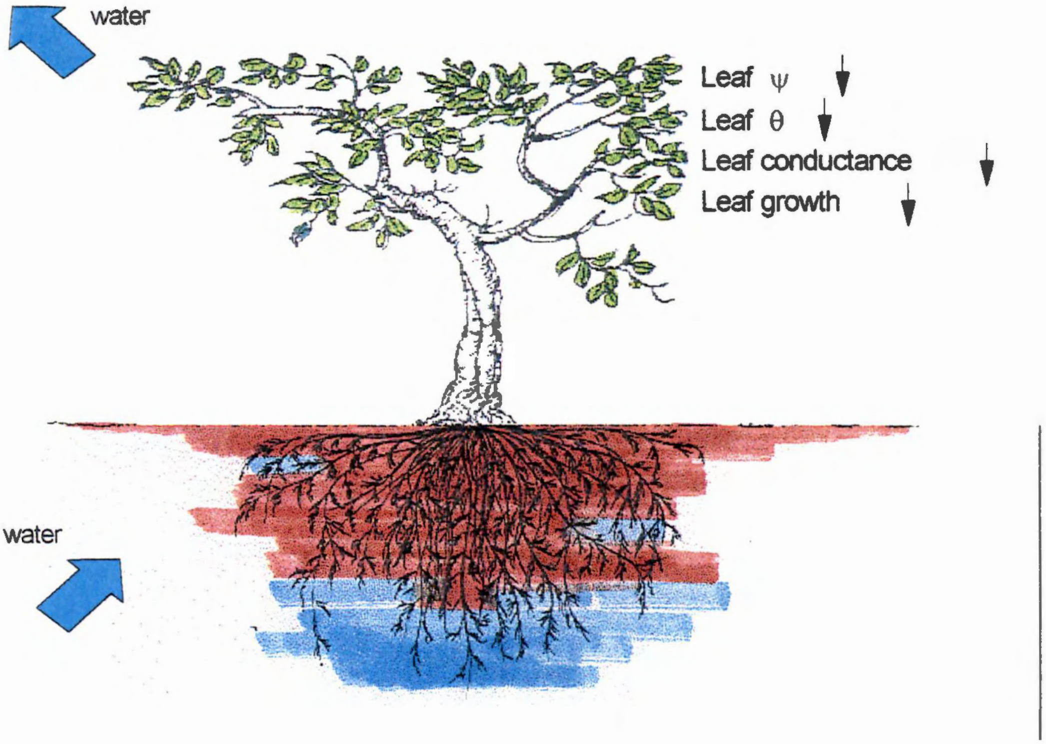


Figure 1-1. Direct, hydraulic limitation.

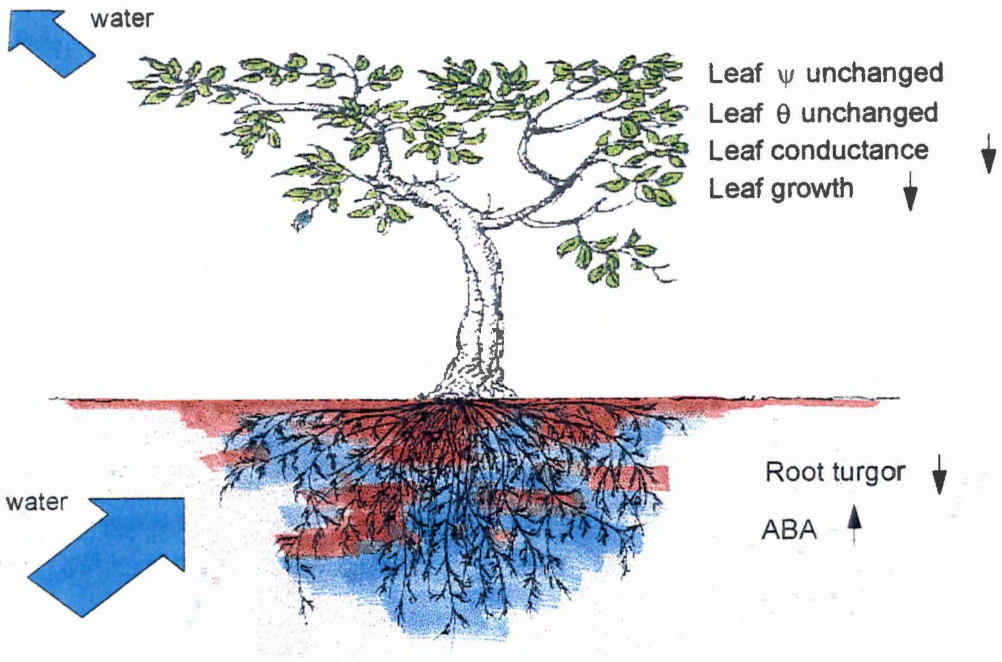


Figure 1-2. Nonhydraulic, root-sourced limitation.

expressed as an alteration of growth or g_s in the leaves (Gowing et al. 1993b). Additionally, in woody (apple) and herbaceous (maize) plants exposed to soil drying, g_s was reduced although leaf Ψ was same or even higher than well-watered plants (Jones 1990b; Blackman and Davies 1985).

There has been debate about the nature of this signal originating in droughted roots. Some researchers have suggested a negative signal, a reduction of a growth promoter such as cytokinin (Davies et al. 1986; Davies and Zhang 1991); however, it has been noted that the magnitude of a purely negative signal would fluctuate with root volume whether or not some roots were in drying soil (Jones 1990a). A second hypothesis is for a positive chemical signal: an inhibitor produced in drying roots, transported via the xylem, resulting in reduced growth and g_s (e.g. Zhang et al. 1987). The later hypothesis is supported by research showing that growth inhibition was alleviated by excision of droughted roots, indicating that it was an inhibitory signal produced by the drying roots (Gowing et al. 1990).

Such nonhydraulic signaling of drying has been observed in many herbaceous species including corn (Saab and Sharp 1989; Tardieu et al. 1991), cowpea (Bates and Hall 1981; Ebel et al. 1996), maize (Zhang and Davies 1989), rice (Bano et al. 1993), sorghum (Ebel et al. 1994), sunflower (Neales et al. 1989) and wheat (Blum et al. 1991). While nonhydraulic signaling has been well documented for herbaceous species, Saliendra et al. (1995) argue that nonhydraulic signaling may not be a significant drought mechanism for woody species because it would be an inefficient mechanism for rapid stomatal control due to lengthy transport time.

Nonhydraulic signaling has been reported in woody species by other researchers [e.g. Douglas-fir (Blake and Ferrell 1977), apple (Gowing et al. 1990), rose (Augé and Duan 1991), sycamore (Khalil and Grace 1993) and some conifer species (Jackson et al. 1995)]. Also, it seems logical that although nonhydraulic signaling may not play a role in drought strategy of large, mature tree species, it may be important in seedling development. Drought resistance mechanisms such as dynamic stomatal control are often involved in tree species distribution, mainly because of their role in juvenile establishment and survival (Martin et al. 1987). It has been observed that phenological patterns of growth in seedlings and saplings differ from those of large trees (Hinckley et al. 1981).

Much recent work has focused on identifying the signal and how it works. It has long been known that abscisic acid (ABA) is a potent inhibitor of stomatal opening (Jones and Mansfield 1970), and there is evidence that stomates of droughted plants are more sensitive to ABA (Blackman and Davies 1985). Until recently, it was thought that the first stomatal response during water stress was the result of ABA release from the mesophyll cells of leaves (Zhang and Davies 1987); however, ABA synthesized in drying roots can regulate stomatal behavior, independent of any direct, hydraulic signal (Zhang et al.1987; Zhang and Davies

1989; Tardieu and Davies 1991, 1992).

Increased ABA production has been observed in root tips of pea (*Pisum sativum*) and *Commelina communis* exposed to drying soil (Zhang and Davies 1987). The exact mechanism stimulating production of ABA in roots is unknown, but one idea is that a reduction in soil water potential resulting in turgor loss in root cells leads to increased production of ABA or some other growth regulator (Munns and Sharp 1993). Whatever the mechanism of action, these recent studies indicate that root synthesis of ABA increases in droughted roots; the ABA moves to the leaves by the xylem stream where it then affects leaf physiology and morphology.

The primary effects of xylem ABA produced during water stress on plant physiology appear to be reduced g_s, increased root growth and/or reduced leaf growth. Close relationships between xylem ABA concentration and g_s have been observed in laboratory experiments (Zhang and Davies 1990a, 1990b; Turner 1991) and field experiments (Wartinger 1990; Tardieu et al. 1992a). Xylem ABA concentration was found to be strongly correlated with g_s in maize (Tuberosa et al. 1994). A chemical in the xylem reduced the transpiration rate in water-stressed wheat; however, the chemical was not identified (Munns 1992). In addition to effects on g_s, ABA is involved in differential shoot versus root growth. ABA produced at low water potential stimulated root growth in maize while inhibiting shoot growth (Saab et al. 1990). ABA can also inhibit leaf growth (e.g.

Ludlow et al. 1989; Saab and Sharp 1989; Zhang and Davies 1990a, 1990b; Tardieu et al. 1993).

Neither nonhydraulic nor direct hydraulic control alone may sufficiently explain altered g_s during water stress. Synthesis of ABA is roughly proportional to the root Ψ, thus purely nonhydraulic or direct hydraulic stomatal control may be unlikely (Tardieu and Davies 1993). Stomatal conductance in maize declined with declining leaf Ψ at constant ABA concentrations (Tardieu and Davies 1993). A model incoporating these parameters indicates that a dual control system is feasible and that overall plant water relations may influence chemical signaling by effects on root Ψ and dilution of the chemical signal (Tardieu and Davies 1993; Tardieu 1993). Similarly, Davies et al. (1994) propose an interactive control system in which changes in leaf water status and environmental conditions affect stomatal sensitivity to nonhydraulic signaling. The extent of stomatal response to root-sourced ABA has been observed to vary with leaf water status (Munns and King 1988; Gowing et al. 1993a). There is also evidence that length of drought influences stomatal sensitivity. Medium- and long-term stress caused the stomata of *Commelina communis* to become more sensitive to ABA; also, during long-term stress, the stomata were at first more sensitive, then became less sensitive as the drought continued (Peng and Weyers 1994). Additionally, mycorrhizal symbiosis and nutritional status can alter nonhydraulic signaling (Augé and Duan 1991; Augé et al. 1994; Augé et al.

1995; Ebel et al. 1994).

Though the mechanism of action and the exact effects are still in question, evidence indicates that nonhydraulic, chemical signaling is an important plant response to drought for both herbaceous and woody plants (Davies et al. 1994). The ability to respond to changes in available soil water could improve a plant's long-term water use efficiency and survival (Ludlow et al. 1989; Mansfield and McAinsh 1995). For example, in a study of five hardwood species, species better adapted to drought had a competitive advantage over other species (Bunce et al. 1977).

Nonhydraulic inhibition of g_s may vary among species like other drought strategy characteristics discussed above. Avoiders, which have dehydration sensitive tissues (i.e. leaves die at relatively high leaf Ψ), would theoretically use nonhydraulic signaling to avoid transpirational water loss and potential leaf death during drought. Conversely, tolerators, which have tissues better adapted to withstand dehydration (i.e. leaves die at lower leaf Ψ), often lack or are less sensitive to nonhydraulic signaling.

Most research on nonhydraulic, chemical signaling has focused primarily on the physiological aspects of the process. We proposed to examine the ecological significance of nonhydraulic signaling in the context of drought resistance profiles of six deciduous tree species of the southeastern United States. Trees with roots split between two pots were used to test whether there was a variation among species in sensitivity of stomatal opening and extent of stomatal inhibition due to nonhydraulic signaling. Additionally, we compared the effects of the signal on new versus older leaves and determined the amount of soil drying required before a signal was observed. These data on signaling, along with data from previous research classifying relative dehydration tolerance in several species of deciduous trees, were used to see if species with comparatively less capacity for tolerating leaf dehydration (drought avoiders) showed relatively higher stomatal sensitivity to nonhydraulic signals.

2. Materials and Methods

Plant material

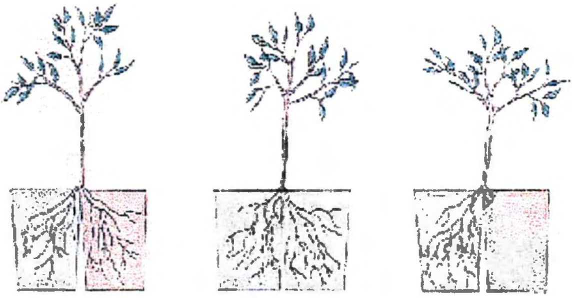
Two- to three- year old saplings of the following species were planted with the root system divided between two 11 liter plastic pots (thirty individuals of each species) in the fall of 1995: red maple (*Acer rubrum* L.), flowering dogwood (*Cornus florida* L.), fringe tree (*Chionanthus virginicus* L.), carolina silverbell (*Halesia carolina* L.), tulip poplar *(Liriodendron tulipifera* L.) and sourwood (*Oxydendrum arboreum* (L.) DC.). All saplings were container-grown from seed obtained from local provenances and ranged in height from about 0.5 to 1.5 m. Standard nursery potting medium was used: 4 pine bark/ 1 sand, to each m^3 was added 4 liters dolomitic lime, 4 liters 17-6-10 osmocote plus minor elements and 2 liters epsom salt ($MgSO_4$). Split-root plants were allowed to overwinter and the experiment was conducted in a 24.4 by 7.3 m shade house (2 layers of 4 ml clear polyethelene stretched over bowed aluminum supports) on the University of Tennessee (Knoxville) nursery compound. The shade house was covered by a 50% transmission shade cloth, to promote stomatal opening. On 5 May 1996, 30 g of 14-14-14 osmocote was added to each pot. The sixteen healthiest plants of each species appearing to have the most evenly divided roots were chosen for the experiment.

All plants were monitored throughout the experiment for nutritional needs and pathogen and insect damage. On 24 June 1996, all *C. florida* trees were fertilized with magnesium to treat chlorosis (MgCl, 3.2 g liter^{-1} water). Beginning on 30 May 1996, and continuing every 9 to 10 days, all plants were sprayed with Talstar (3.9 ml liter^{-1}, bifenthrin, FMC Corporation, Agricultural Chemical Group, Philadelphia, PA) to control spider mites, aphids and thrips. Beginning 19 June 1996 and continuing every 3 weeks, all *C. florida* and *L. tulipifera* individuals were treated for powdery mildew with Systhane 2 EC (Rohm and Haas Co., Philadelphia, PA) at standard label rate (0.4 ml liter^{-1}).

Treatments and environmental conditions

Each species had three split-root treatments (Figure 2-1). Water was withheld from one pot for a sustained drying period for one set of seedlings (WD). A two-control system was utilized as follows. In one set, one half of the root system was left intact and watered while the other half was severed prior to the drought episode (WS). In the second set, both halves of the root system were left intact and were fully-watered (WW).

On 30 June 1996, one half of the root system of four individuals of each species was severed, and drying treatment was begun for all WD trees by withholding water from one pot. Soil matric potential (Ψ_m) declined rapidly (from -0.01 to -0.09 MPa for some *A. rubrum* and *H. carolina* individuals) and g_s was reduced in WS trees relative to WW trees; therefore, on 2 July 1996, all trees were watered to allow WS trees to acclimate to the severing of the roots. Additionally, on 3 and 8 July 1996, all WD and WS trees were pruned (excluding



half-dried **control 1 fully-watered** **control 2 half-severed**

Figure 2-1. Split-root treatments. Half of the roots of half-severed (WS) controls were excised 12 days before the drying episode began (30 June). Water was withheld from one pot of half-dried (WD) saplings on day 0 (11 July). Both pots of fully-watered (WW) controls were watered throughout the experiment.

C. virginicus and *O. arboreum*), removing about half of the foliage in order to slow the drying rate by reducing the evaporative demand. Pruning did not seem to alter g_s to a large extent (Figures 2-2 and 2-3). On 11 July 1996 ("day 0"), the drying episode was initiated a second time by withholding water from one pot of all WD individuals; this drying period continued until 13 September 1996.
All other pots were watered as needed throughout the experiment, about every other day.

Air temperature and PPFD were recorded throughout the experiment with thermocouples and quantum sensors (LI-189, LiCor, Lincoln, Nebraska), connected to a datalogger (21x, Campbell Scientific, Logan, UT). Air temperature and PPFD were measured every 10 minutes (hourly means

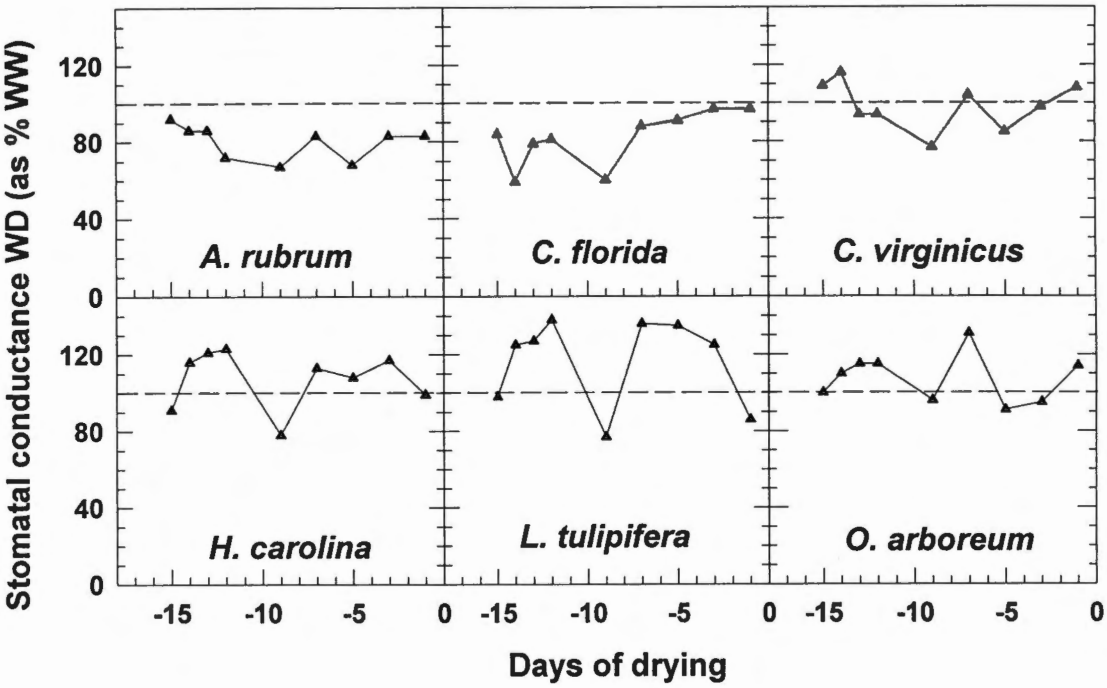


Figure 2-2. Stomatal conductance of WD as % WW just before and after pruning. The relative g_s of each WD tree was computed as its absolute g_s for that day (average of four leaves) divided by the average absolute g_s of the four WW trees of that species for that day, multiplied by 100: WD relative g_s = (WD absolute g_s) / (WW average absolute g_s) * 100. All WD and WS trees were pruned (excluding *C. virginicus* and *O. arboreum*) on days -3 and -8 (3 and 8 July) and water was withheld from WD plants beginning day 0 (11 July).

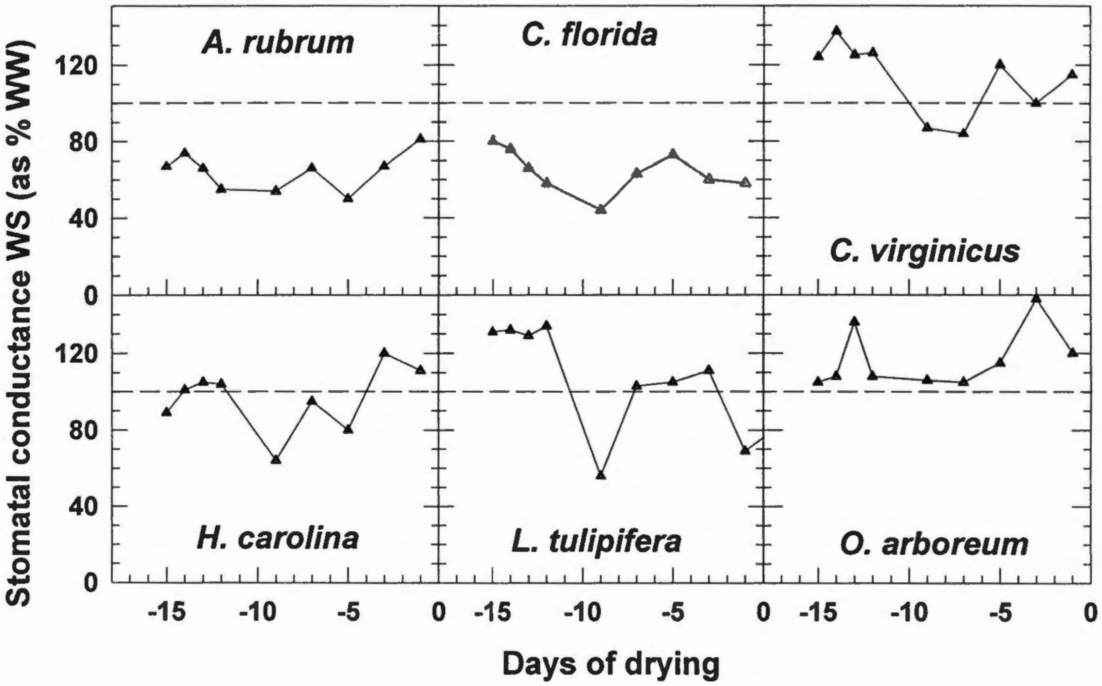


Figure 2-3. Stomatal conductance of WS as % WW just before and after pruning. All WD and WS trees were pruned (excluding *C. virginicus* and *O. arboreum*) on days -3 and -8 (3 and 8 July) and water was withheld from WD plants beginning day 0 (11 July).

recorded), and daily maximum and minimum air temperatures and daily maximum PPFD were calculated.

Water status measurements

Soil Ψ_m was measured every 4 h throughout the drying period for the dried pots of WD plants using heat dissipation soil Ψ_m sensors (SoilTronics, Burlington, WA) connected to a datalogger (21x, Campbell Scientific, Logan, UT) through multiplexers (AM32, Campbell Scientific, Logan, UT). Air dry calibration of soil sensors was obtained on 7-9 May 1996, after allowing insulated sensors to equilibrate on the lab bench overnight. Each sensor was coated with a slurry of kaolinite (a non-swelling clay which improves hydraulic conductivity between sensor and soil) and on 21 May 1996, sensors were buried in pots from which water would be withheld for WD individuals of each species about 7-9 cm from the perimeter of the pot and 12 cm deep. Sensors consisted of a thermocouple and a heating element (evanohm wire, 0.076 mm diameter) housed in a fixed, porous, ceramic cylinder (diameter 1.5cm, length 3.0 cm). Rate of heat dissipation within the ceramic housing is correlated with soil Ψ_m as follows. The temperature of the ceramic is measured at 1 s and 21 s during a 21-s heat pulse. The temperature rise in the ceramic resulting from the heat pulse is a function of its moisture content, or Ψ_m: the drier the ceramic (the lower its Ψ_m), the slower heat will dissipate. If the ceramic housing is in equilibrium with the soil surrounding it (if ceramic Ψ_m = soil Ψ_m), then the temperature rise of the ceramic is directly dependent on soil Ψ_m. Estimates of Ψ_m are independent of soil type and, at constant soil water content, do not vary with temperature between 0 and 40° C. Sensors were calibrated by the manufacturer by relating temperature rise to soil Ψ_m in soil having few solutes (negligible osmotic pressure). Soil Ψ_m between 0 and -0.02 MPa was measured with a hanging water column, soil Ψ_m between -0.02 and -0.10 MPa with a pressure plate (Soilmoisture Equipment Corp., Santa Barbara, Cal., USA) and soil Ψ ($\approx \Psi_m$) between -0.10 and -20 MPa with a thermocouple psychrometer (SC-10; Decagon Devices) (Augé et al. 1994).

Stomatal conductance (g_s) was measured with a diffusion porometer (AP4, Delta-T Devices, Cambridge, UK). On 21 June 1996, g_s was measured diurnally (three individuals of each species, three leaves per individual, hourly from 0800 to 1800 EST, Figure 2-4).

Preliminary, pre-drying g_s measurements of all plants were used to determine the time of day during which g_s was reasonably constant, and hence when g_s would be measured during the drying episode. Stomatal conductance was measured every other day from about 0900 to 1400 h EST. Stomatal conductance was measured at midleaf, parallel to the midvein for four leaves of each individual: the two newest, fully expanded leaves and the two next older, lateral leaves. Up to eight leaves may have been measured each day for an individual, to determine the highest g_s for the newest leaves. To control for possible diurnal effects, g_s was sampled in a specific order each day: one WW,

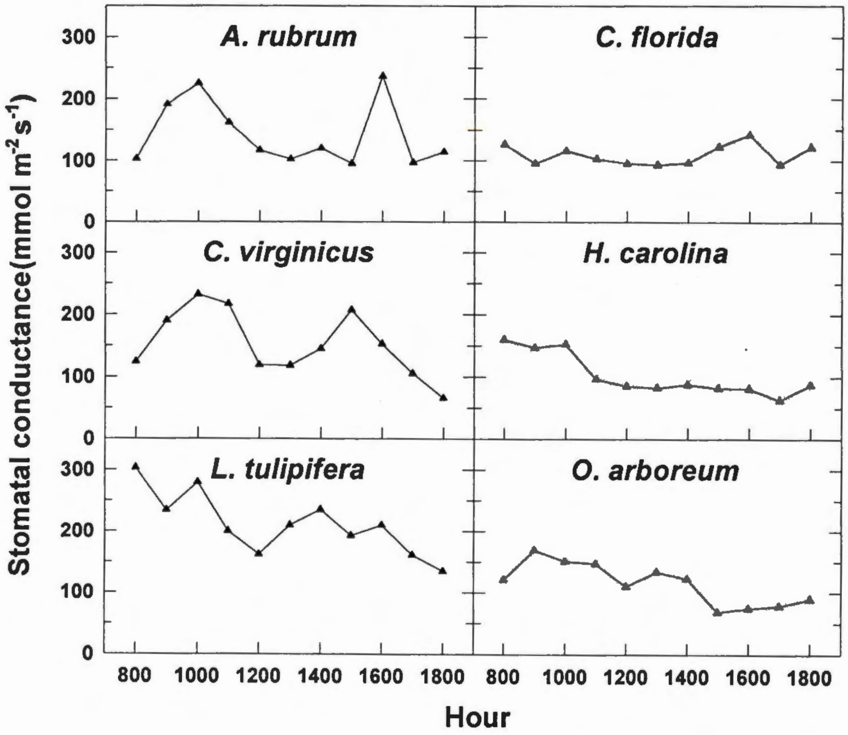


Figure 2-4. Diurnal measurement of stomatal conductance, 21 June 1996. Points represent hourly means (n = 3).

one WD, one WS and one WD plant was measured for a species, then one WW, one WD, one WS and one WD plant for another species, etc. Once four plants of each species had been sampled this way the pattern was repeated until all replicates of each species were measured. Each day the species order and treatment sampling order were maintained, but initial species was shifted (i.e. day one: *A. rubrum, C. florida, C. virginicus*, ...; day two: *C. florida, C. virginicus, H. carolina*,...etc.).

Beginning 18 July 1996 and continuing for all g_s measurement days, one leaf from each individual was collected for analysis of osmotic potential (Ψ_π). Beginning on 6 August 1996, two *O. arboreum* plants and four *C. virginicus* plants were sampled only once a week due to limited foliage remaining. After 14 August 1996, about half of the plants in the experiment were also only sampled once a week for the remainder of the experiment because it was estimated that if sampling continued until September or mid-October, two-thirds or more of the leaf area would be removed. Leaves were immediately placed in a syringe, frozen in liquid nitrogen and stored in an ultra-low (-80 ° C) freezer, pending later analysis of Ψ_π using a vapor pressure osmometer (Model 5500 XR, Wescor Inc.; Logan, UT). All Ψ_π for collected samples were determined from 7 August through 4 December 1996. The osmometer was calibrated daily with graded NaCl solutions. Syringes were removed from the freezer and allowed to thaw until no longer cold to the touch (10-15 minutes) before measuring Ψ_{π}. Thawing time was kept consistent among samples to minimize changes in sap composition among treatments which might alter Ψ_π.

On 9 September 1996, roots of all plants having soil Ψ_m of -0.02 MPa or lower were excavated. The drying period ended on 13 September 1996, and roots of remaining plants were excavated. Roots were dried at 80 °C for one week and then weighed, to determine how evenly roots were divided between the two pots and to compare the size of the root systems among treatments.

Experimental design and statistical analysis

We used a six (species) x three (treatments) factorial design. For each species, sixteen of the healthiest plants appearing to have the most evenly divided root systems were identified, then eight were randomly selected for the WD treatment, four for the WS treatment and four for the WW treatment. Plants were arranged in three blocks around the datalogger with treatments and species randomized in each block. Means were separated within each species using the General Linear Models Procedure for ANOVA (SAS, Cary, NC). ANOVA included linear contrasts of g_s among treatments for each day measurements were recorded for each species. Regression and correlation analysis were used to define and describe relationships between relative g_s and declining soil Ψ_m for each species.

3. Results

Root dry weights

Root dry weights were compared for both halves of the root system of all individuals to estimate relative water gathering capacity among species (Figure 3-1). To conclude that nonhydraulic signaling inhibited g_s in half-dried plants, rather than direct hydraulic limitations alone, we included a control with about the same water gathering capacity as WD plants. The WS plants were used as our primary control rather than WW plants, which received twice as much water as WD plants, thus potentially having different fluctuations in plant water status than the WD and WS treatments. Mean root dry weights of the watered side of WS saplings were similar ($P \leq 0.05$) to mean root dry weights of the watered side of WD plants for all species (Figure 3-1).

Stomatal conductance versus time

Drying resulted in reduced g_s of WD plants relative to WS and WW controls for all species for most days during the drying episode (Figures 3-2 and 3-3). These values were calculated by dividing the eight individual WD plants for each species by the mean of all WS plants of a given species (mean of four leaves per plants), then the eight ratios were meaned to obtain relative g_s. Stomatal conductance of WD relative to WS plants stayed low over the course of the experiment for *C. florida, C. virginicus* and *L. tulipifera*; however, relative g_s of

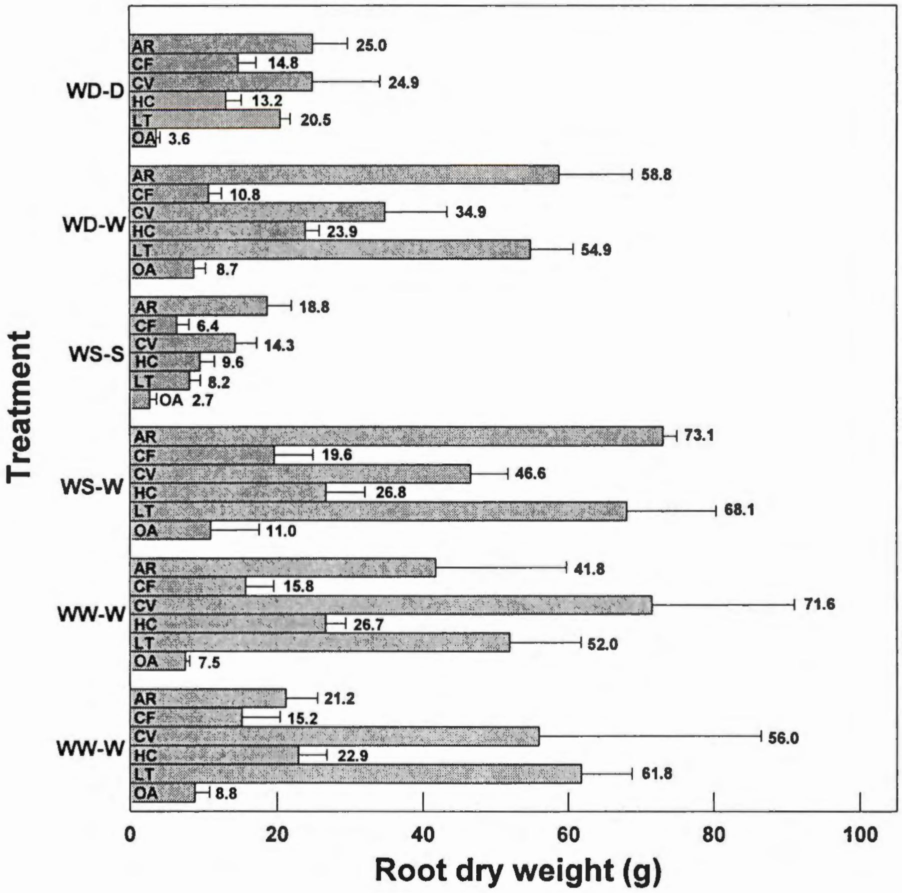


Figure 3-1. Mean root dry weight for dried and watered pots of half-dried (WD, n = 8), severed and watered pots of half-severed (WS, n = 4), and both watered pots of fully-watered (WW, n = 4) treatments. Values are means for each species and bars are standard errors.

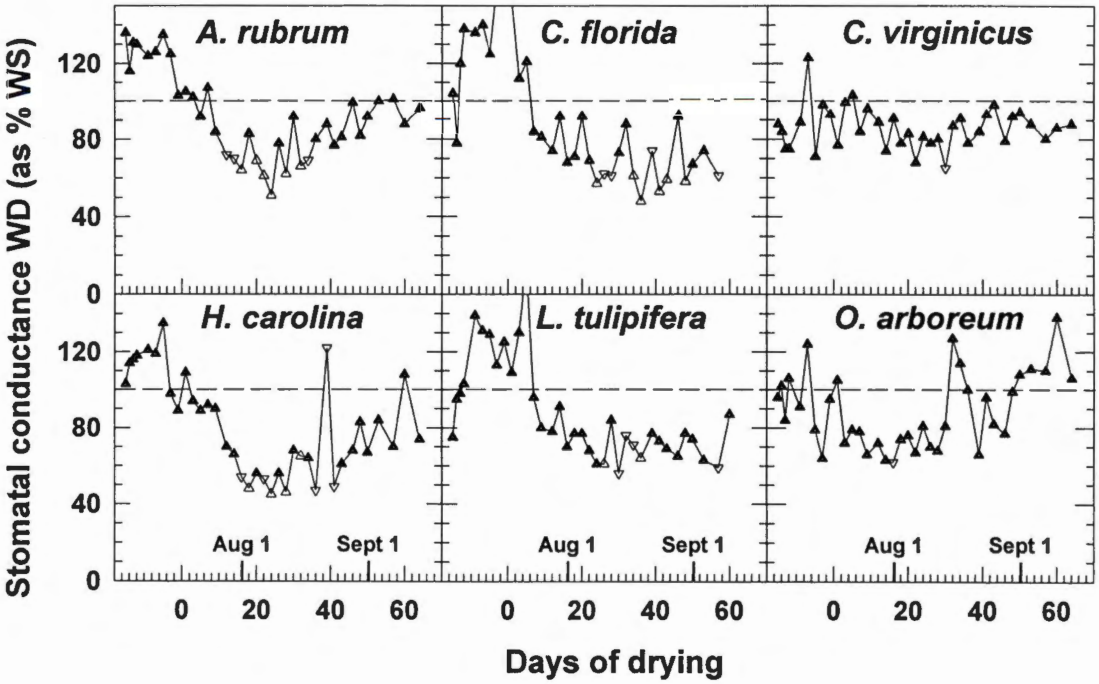


Figure 3-2. Stomatal conductance of WD saplings relative to WS controls. Relative g_s of each WD tree was computed as its absolute g_s for that day (average of four leaves) divided by the average absolute g_s of the four WS trees of that species for that day, multiplied by 100: WD relative g_s = (WD absolute g_s) / (WS average absolute g_s) * 100. Symbols indicate means significantly different from controls (▲ : NS, △ : $P \leq 0.05$, ▽ : $P \leq 0.10$). Roots in one pot of WS plants were severed on day -12 (30 June). Plants were fully-watered until day 0 (11 July), when water was withheld from one pot of WD plants.

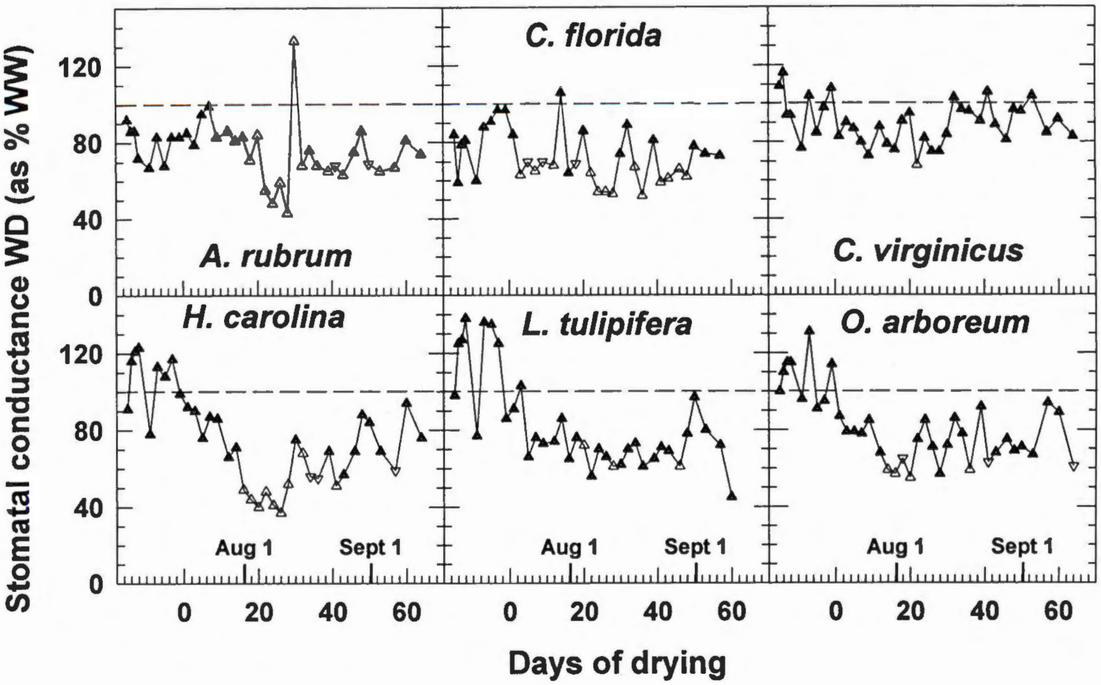


Figure 3-3. Stomatal conductance of WD saplings relative to WW controls (individual WD / mean WW). Points represent daily means of eight WD individuals, four leaves per plant. Symbols indicate means significantly different from controls (▲ : NS, Δ : $P \leq 0.05$, ∇ : $P \leq 0.10$).

WD plants of *A. rubrum*, *H. carolina* and *O. arboreum* began to increase near the end of the drying period (Figure 3-2).

Stomatal conductance of WS controls was mostly similar to that of the WW controls (Figure 3-4). Stomatal conductance of WS relative to WW plants was different ($P \leq 0.05$) for one only day of the drying period for *A. rubrum, C. viginicus, L. tulipifera* and *O. arboreum*, and was not different on any day for *H. carolina*. There were additional differences ($P \leq 0.10$) for *A. rubrum* and *O. arboreum*. Stomatal conductance of WS saplings relative to WW saplings dropped temporarily in *A. rubrum, C. florida* and *L. tulipifera* early in the experiment due to root excision (WS means were different from WW means on day -3 for *A. rubrum* ($P \leq 0.10$), days -3 to 5 for *C. florida* ($P \leq 0.05$) and day 5 for *L. tulipifera* ($P \leq 0.10$).

Absolute g_s of *A. rubrum*, *C. virginicus* and *L. tulipifera* saplings fluctuated more than g_s of *C. florida, H. carolina* and *O. arboreum* throughout the experiment (Figure 3-5). Fluctuations were fairly consistent from day to day among treatments, thus were probably due to variations in environmental conditions in the shade house, such as humidity, irradiance and temperature (Figure 3-6).

Stomatal conductance versus soil matric potential

Species varied in maximum amount of inhibition, soil Ψ_m at which inhibition was first observed and in duration of inhibition. Relative g_s of the WD

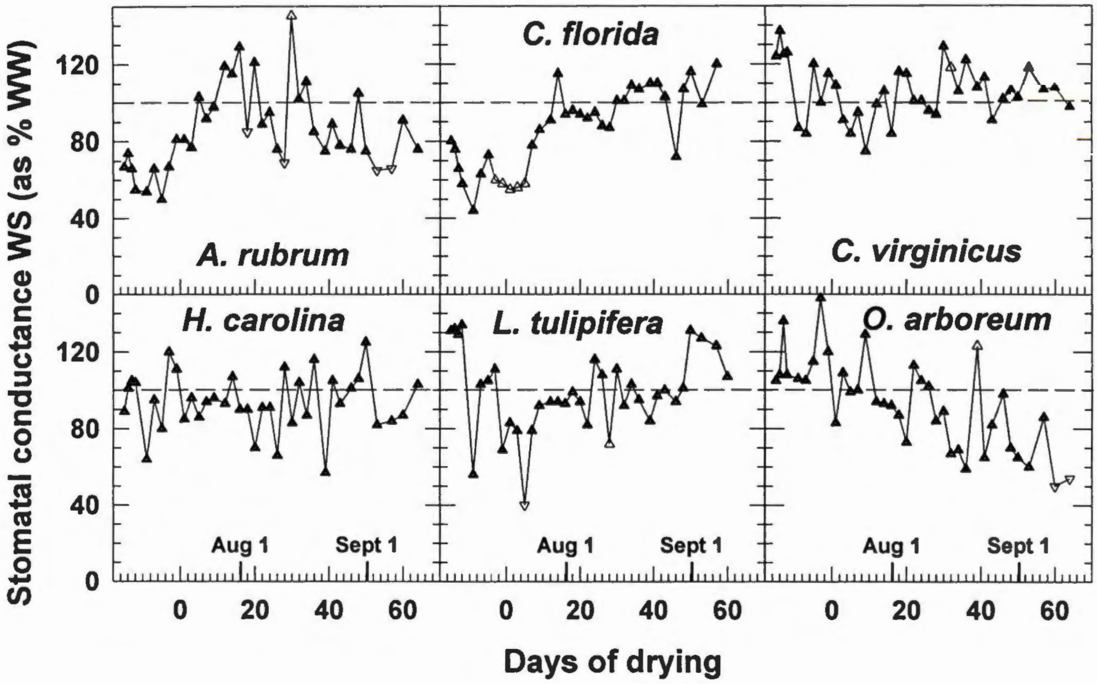


Figure 3-4. Stomatal conductance of WS saplings relative to WW controls (individual WS / mean WW). Points represent daily means of four WS individuals, four leaves per plant. Symbols indicate means significantly different from controls (▲ : NS, △ : $P \leq 0.05$, ▽ : $P \leq 0.10$).

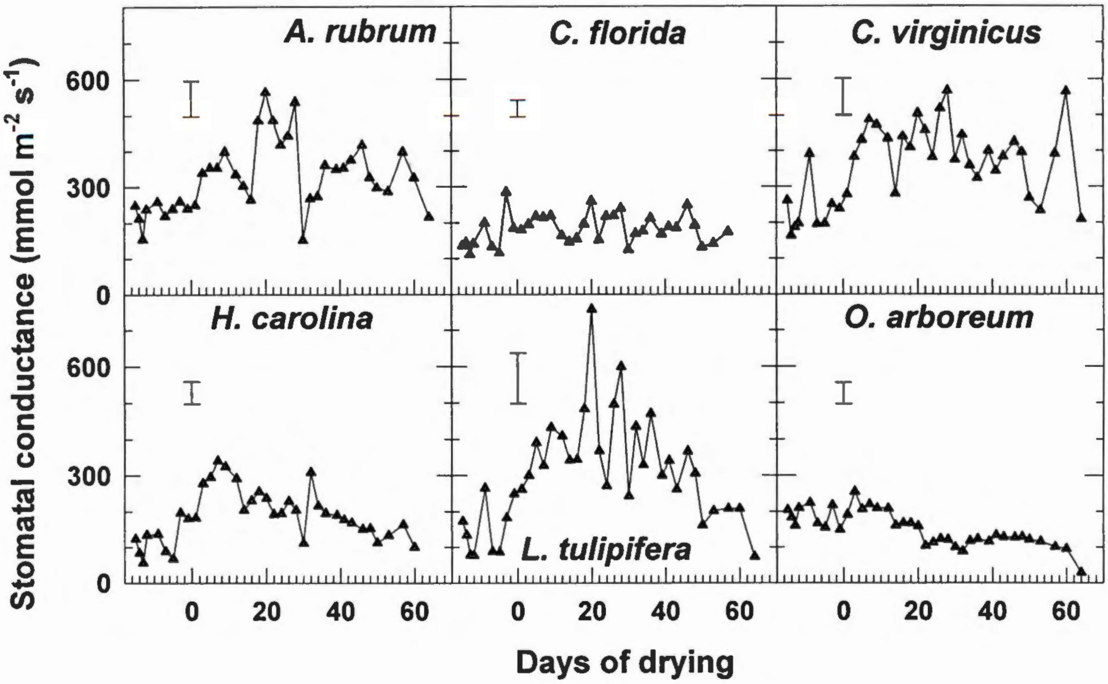


Figure 3-5. Stomatal conductance of fully-watered (WW) saplings (both pots watered throughout experiment). Points represent daily means (n = 4). Water was withheld from half-dried (WD) saplings beginning day 0 (11 July).

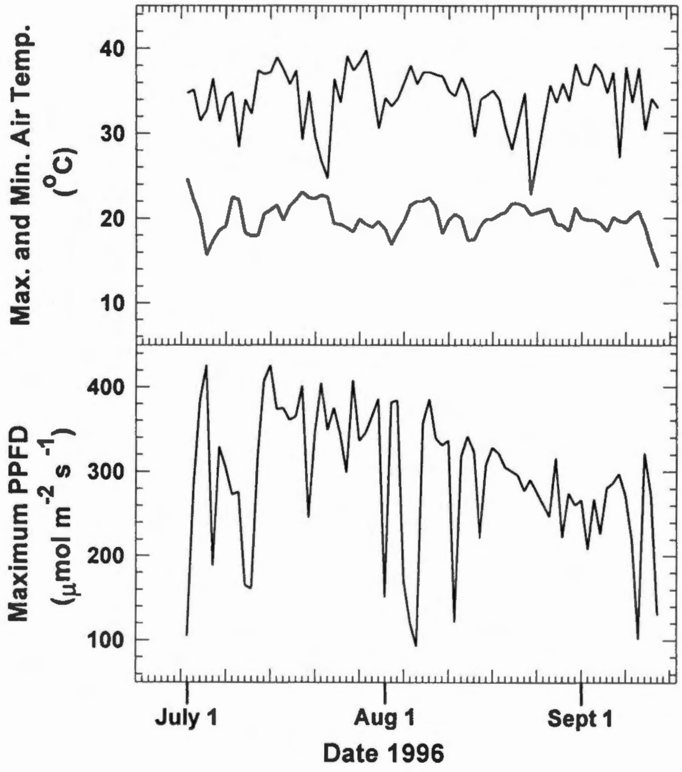


Figure 3-6. Air temperature and PPFD in the shade house during the experiment. These data were collected every 10 minutes and integrated hourly. Shown are maximum (air temperature and PPFD) and minimum (air temperature) hourly means for each day.

treatment of *L. tulipifera* and *H. carolina* reached the lowest values among species, followed by *A. rubrum* and *C. florida* (Table 3-1). Relative g_s of *C. virginicus* and *O. arboreum* was least inhibited among species. Although *O. arboreum* had the least stomatal inhibition, this species seemed to respond with the least soil drying to signaling, reaching 80% g_s at mean soil Ψ_m of 13 kPa. *H. carolina* and *C. virginicus* were intermediate in amount of soil drying required to produce a signal; both reached 80% g_s at soil Ψ_m of about 26 to 27 kPa. *L. tulipifera* and *C. florida* required slightly more drying to produce a signal, reaching 80% g_s at around 32 to 33 kPa. *A. rubrum* required the most soil drying to reach 80% g_s (44 kPa).

Inhibition of g_s occurred in all species before soil Ψ_m dropped to a level detectable as different from fully-watered soil (Figure 3-7). Relative g_s of WD plants *C. florida, H. carolina* and *L. tulipifera* declined as soil Ψ_m dropped below -0.01 MPa and remained inhibited below -1.0 MPa. Stomatal conductance of *A. rubrum, C. virginicus* and *O. arboreum* also declined initially as soil dried below -0.01 MPa; however, g_s recovered as soil Ψ_m reached -0.1 to -1.0 MPa. As soil drying became more severe, nonhydraulic, chemical signaling may have stopped due to reduced water flow from drying roots.

Relative g_s of WD plants declined most rapidly in *L. tulipifera*. *A. rubrum* and *C. florida* had similar rates of decline in g_s and extent of inhibition (Figure 3-8). Stomatal conductance of WD relative to g_s of WS was correlated with declining soil Ψ_m for *A. rubrum* ($r = 0.89^{P \leq 0.0005}$), *C. florida* ($r = 0.65^{P \leq 0.03}$), *C.*

Table 1. Soil Ψ_m at WD g_s 0.80 of WS controls and maximum inhibition of WD g_s expressed as percent of WS controls. Maximum inhibition values were computed by ordering all relative g_s measurements for all days after day 0 and averaging the lowest 20% of these, for each species. Letters following maximum inhibition values indicate statistically similar means ($P \leq 0.05$). Maximum inhibition values for *C. virginicus* and *O. arboreum* may have been lower had these two species dried soil to a larger extent (to a lower soil Ψ_m) than was observed in this experiment.

Species	**Soil Ψ_m at 80% g_s (kPa)**	**Maximum inhibition (% WS)**
A. rubrum	44	47 ab
L. tulipifera	33	38 bc
C. florida	32	48 ab
H. carolina	27	31 c
C. virginicus	26	57 a
O. arboreum	13	57 a

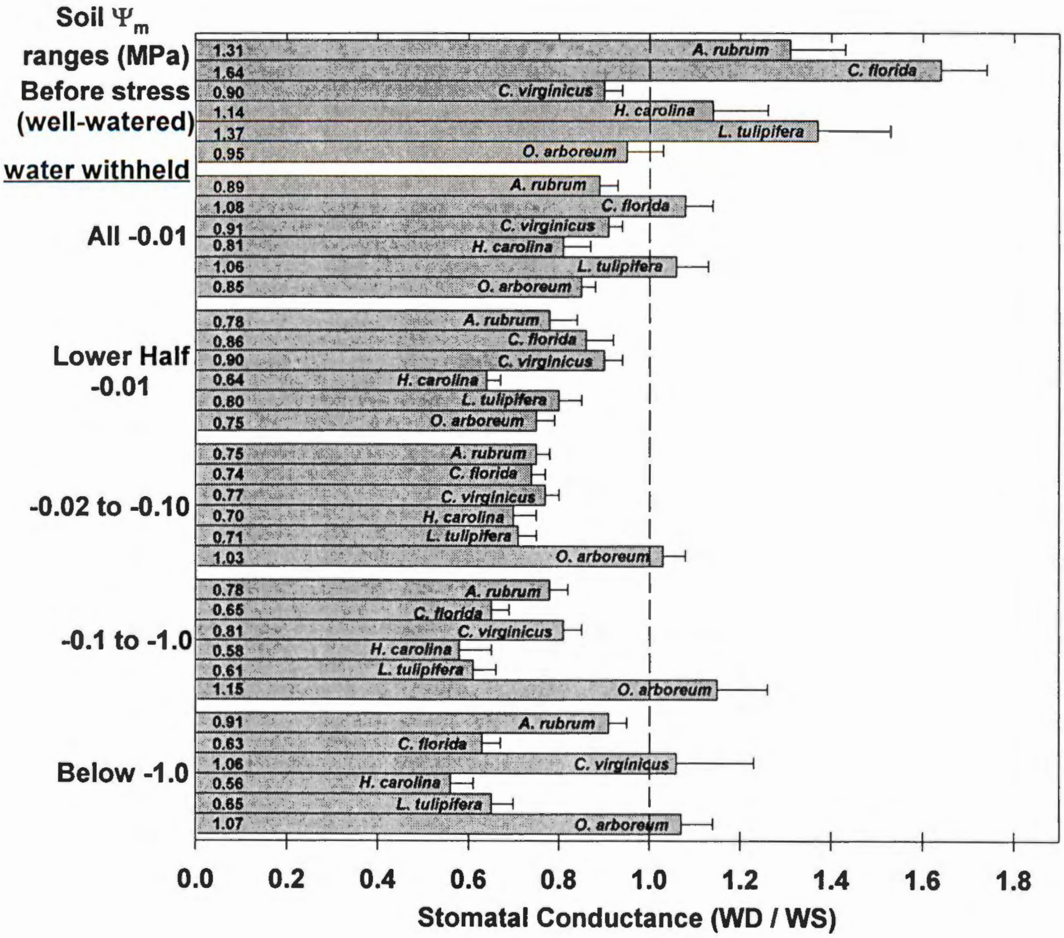


Figure 3-7. Stomatal conductance of WD saplings relative to WS controls at increasing levels of soil drying. Soil Ψ_m ranges are as follows: 1) g_s before water was withheld from WD plants, 2) g_s for all plants at soil Ψ_m of -0.01 MPa, 3) g_s for plants in the lower (i.e. drier) half of all plants at soil Ψ_m of -0.01 MPa, 4) g_s of all plants at soil Ψ_m from -0.02 to -0.10 MPa, 5) g_s of all plants at soil Ψ_m from -0.10 to -1.0 MPa, and 6) g_s of all plants at soil Ψ_m lower than -1.0 MPa. Values within shaded bars are means of individual saplings (n = 3 to 120). Lines above bars represent standard errors of WD means.

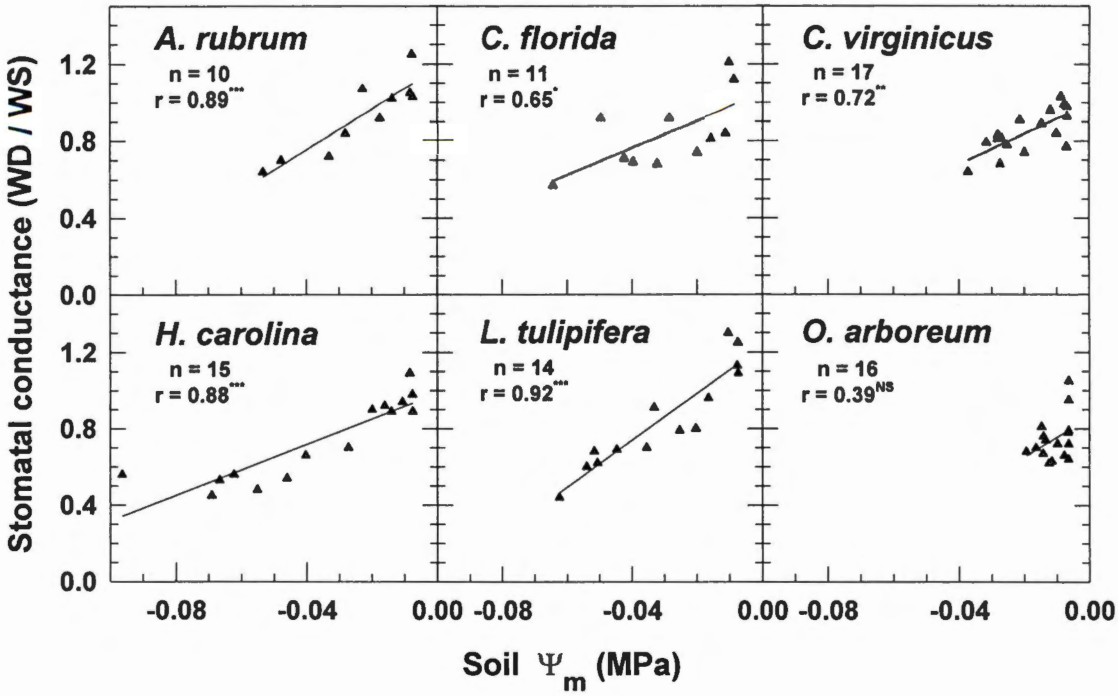


Figure 3-8. Relationship between g_s of WD relative to WS saplings and soil Ψ_m. Points represent daily means (n = 8) and number of points regressed are indicated for each species. Symbols indicate significance of correlations (*** $P \leq 0.0001$, ** $P \leq 0.001$ and * $P \leq 0.05$).

virginicus ($r = 0.72^{P \leq 0.001}$), *H. carolina* ($r = 0.88^{P \leq 0.0001}$) and *L. tulipifera* ($r = 0.92^{P \leq 0.0001}$). There was no correlation between g_s and soil Ψ_m for *O. arboreum* ($r = 0.39^{NS}$). Stomatal conductances of *H. carolina* and *L. tulipifera* were inhibited to about the same extent; although g_s of *L. tulipifera* declined more rapidly and reached maximum inhibition at a higher soil Ψ_m.

Once inhibited, absolute values of g_s did not decline further as soil Ψ_m dropped below -1 MPa for *A. rubrum, C. florida, H. carolina* and *L. tulipifera* (Figure 3-9), and below -1.0 MPa, relative g_s and soil Ψ_m were not correlated. Absolute values of g_s also remained fairly constant in the 0 to -0.1 MPa range for all species (Figure 3-10); although for most individuals, g_s was reduced relative to WS controls.

Soil drying rates differed among species and among individuals within each species (Figure 3-11). *C. virginicus* and *O. arboreum* had the slowest rate of drying and least extensive amount of drying among species, both reaching soil Ψ_m different from well-watered soil on day 53 of the drying episode (mean soil Ψ_m on day 53 for *C. virginicus:* -0.26 MPa, for *O. arboreum*: -0.82 MPa; Figure 3-12). Soil Ψ_m of *A. rubrum, C. florida* and *L. tulipifera* declined most rapidly and to the largest extent among species. Soil Ψ_m began declining on day 40 of withholding water for *A. rubrum* (mean soil Ψ_m -2.04 MPa) and day 39 for *C. florida* (mean soil Ψ_m -2.06 MPa) and *L. tulipifera* (mean soil Ψ_m -2.66 MPa). Soil Ψ_m of *H. carolina* began to decline on day 43 of withholding water (mean soil Ψ_m -2.29 MPa) and most individuals of this species dried to below -4 MPa (Figure 3-11).

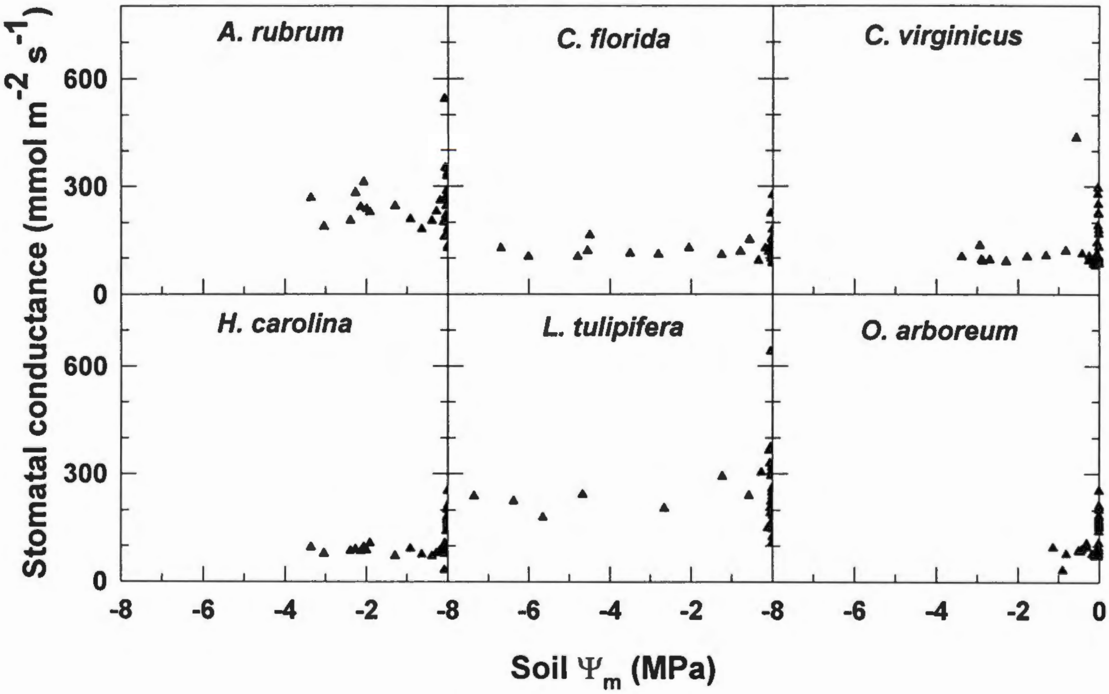


Figure 3-9. Stomatal conductance of WD saplings as soil Ψ_m declined to lowest values reached during the drying period. Points represent daily means (n = 8).

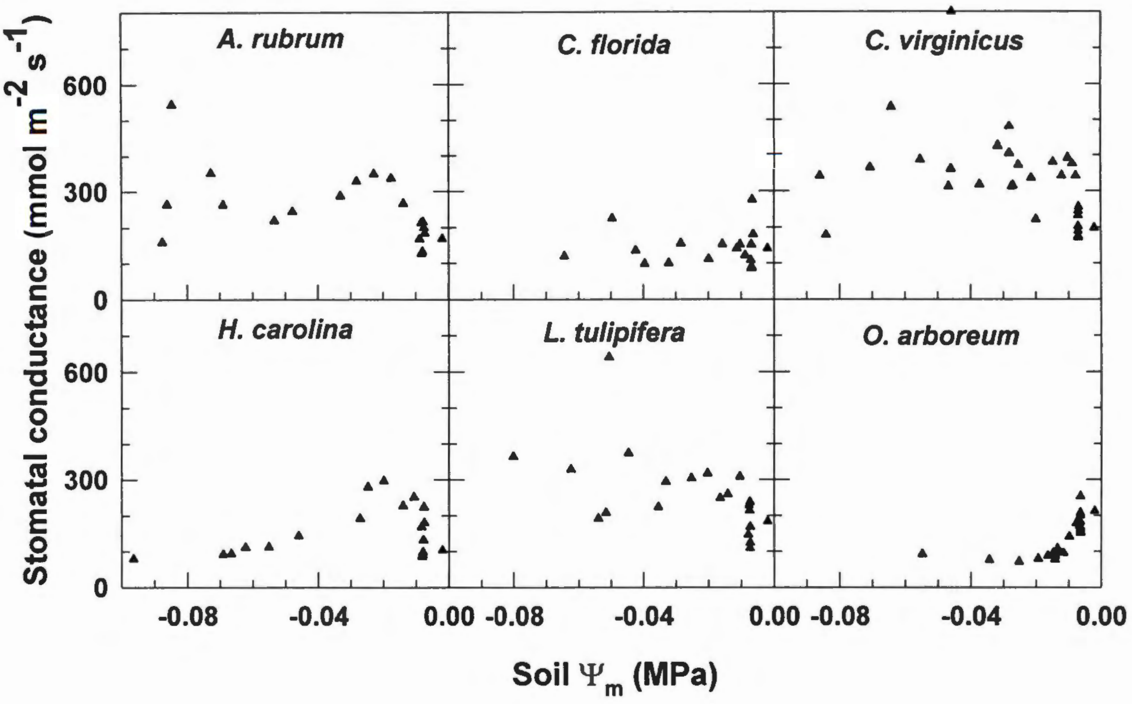


Figure 3-10. Stomatal conductance of WD saplings as soil Ψ_m first began to decline during the drying period. Points represent daily means (n = 8).

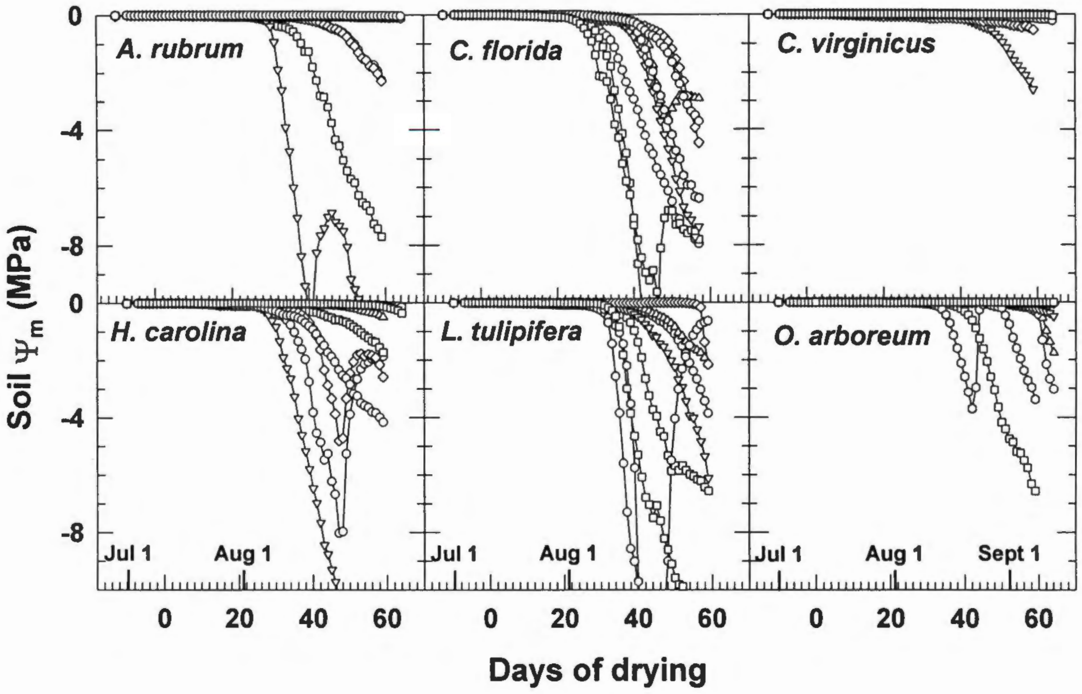


Figure 3-11. Soil Ψ_m of individual WD saplings (n = 8) of each species throughout the drying period. Water was withheld from WD saplings beginning day 0 (11 July).

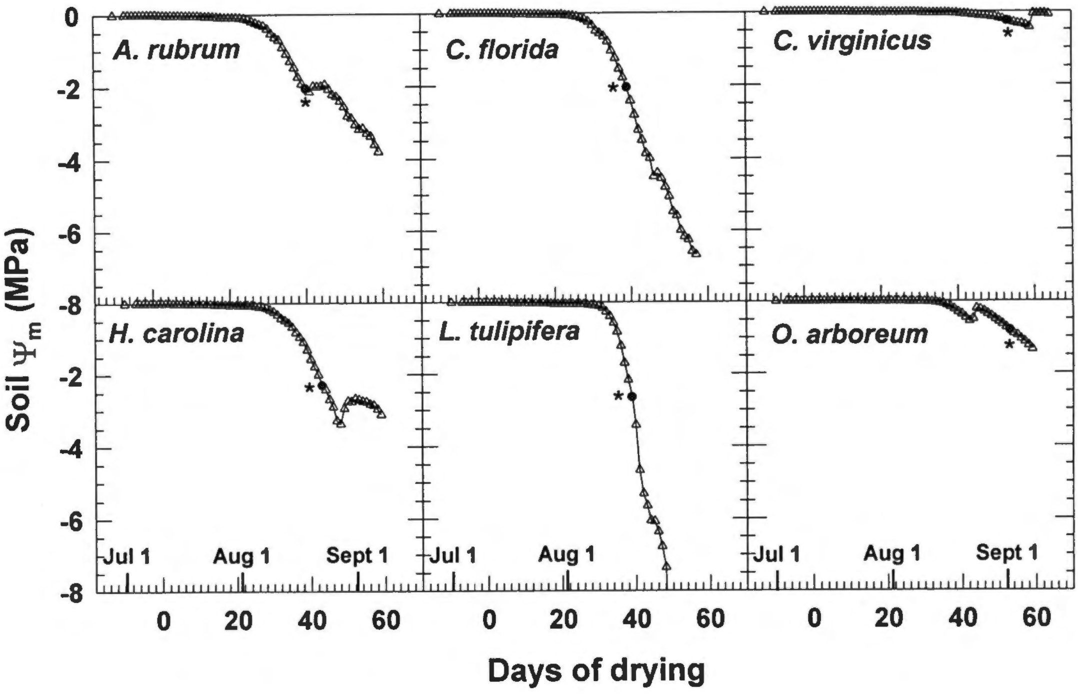


Figure 3-12. Mean soil Ψ_m of WD saplings throughout the drying episode. Points represent daily means (n = 8). Water was withheld from WD saplings beginning day 0. Symbols (*) indicate first day soil Ψ_m was different from soil Ψ_m of fully-watered soil ($P \leq 0.05$), an d on all subsequent days, soil Ψ_m was significantly different from fully-watered soil.

Leaf osmotic potential

Leaf Ψ_π was similar for most days of the drying episode among treatments (there were no differences ($P \leq 0.05$) for *A. rubrum, H. carolina* and *L. tulipifera* among treatments for any day; Figure 3-13). As noted earlier, WS replicates of *C. florida* were most affected among species by root excision; thus differences in leaf Ψ_π for *C. florida* saplings were likely a result of temporary stress due to root severing. Leaf Ψ_π of WD plants remained constant as soil dried (Figures 3-14 and 3-15). Although WS and WD individuals were receiving half as much water as WW plants, the leaf Ψ_π for all treatments was essentially the same throughout the experiment (Figure 3-13). These data indicate that the WD plants were receiving enough water to maintain leaf Ψ_π similar to both WS and WW control plants.

Leaf age comparisons

Stomatal conductances varied with leaf age in *A. rubrum, H. carolina* and *O. arboreum*. For *H. carolina* and *O. arboreum*, the two newest leaves had much lower g_s relative to the two next newest leaves for all three treatments for most of the experiment (Figures 3-16 to 3-18). The leaf age difference was similar for *A. rubrum* and *H. carolina*; however, the difference did not occur until later in the experiment for *A. rubrum* (Figure 3-16). There did not appear to be any large differences in g_s for the two newest compared to the two next newest leaves for any treatment of *C. virginicus, C. florida* or *L. tulipifera*. However,

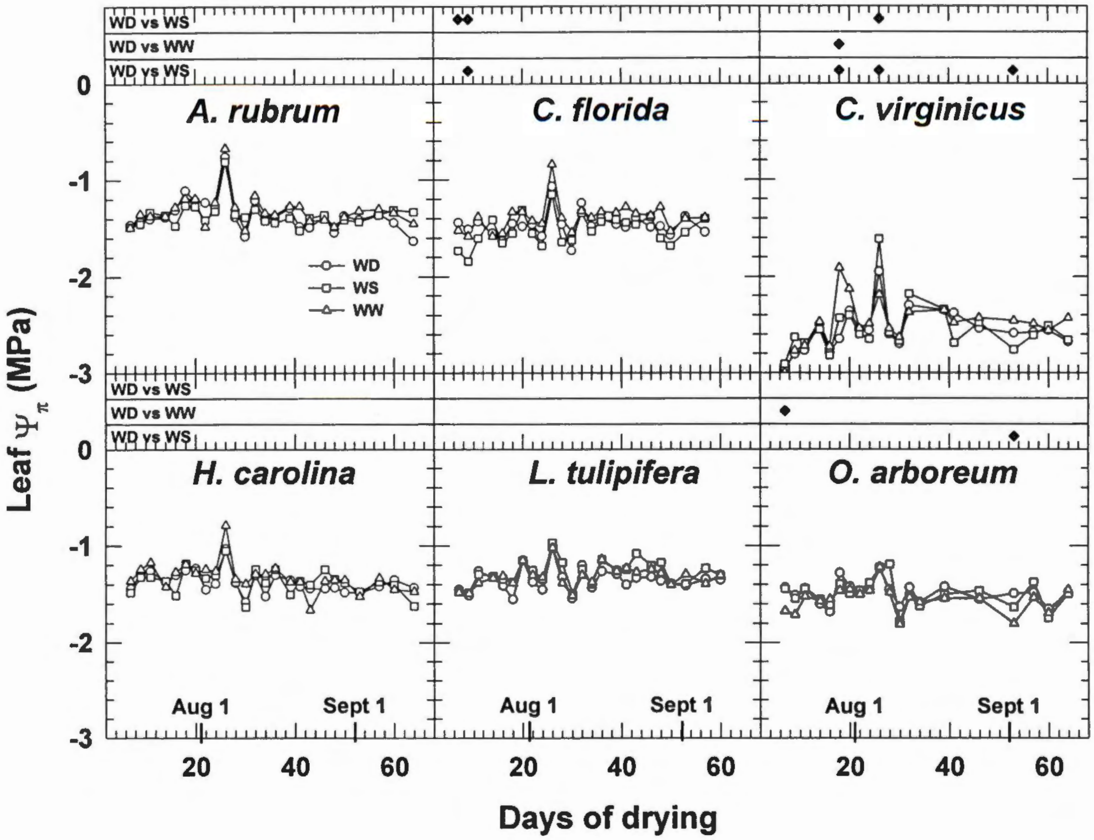


Figure 3-13. Leaf Ψ_π during the experiment for all treatments. Points represent daily means (WD, n = 8; WS and WW, n = 4). Tables above graphs show results of linear contrasts; symbols denote significant differences between treatments on a given day ($P \leq 0.05$). Water was withheld from WD saplings beginning day 0 (11 July).

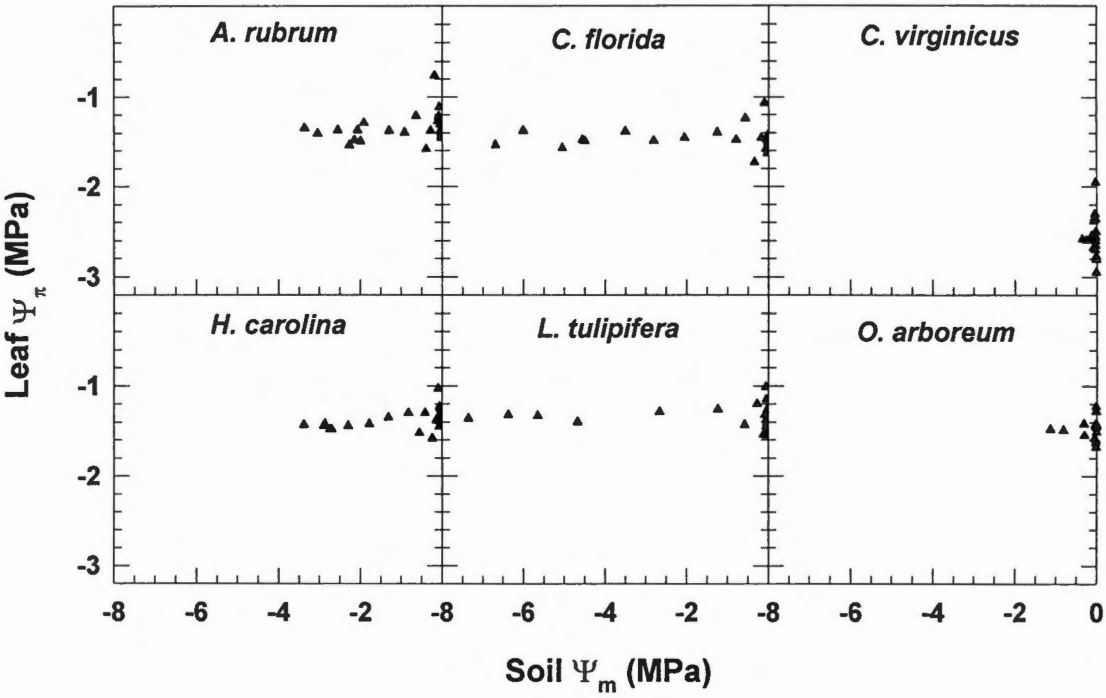


Figure 3-14. Leaf Ψ_π of WD saplings as soil Ψ_m declined to lowest values reached during the drying period. Points represent daily means for both leaf Ψ_π (n = 8) and soil Ψ_m (n=8).

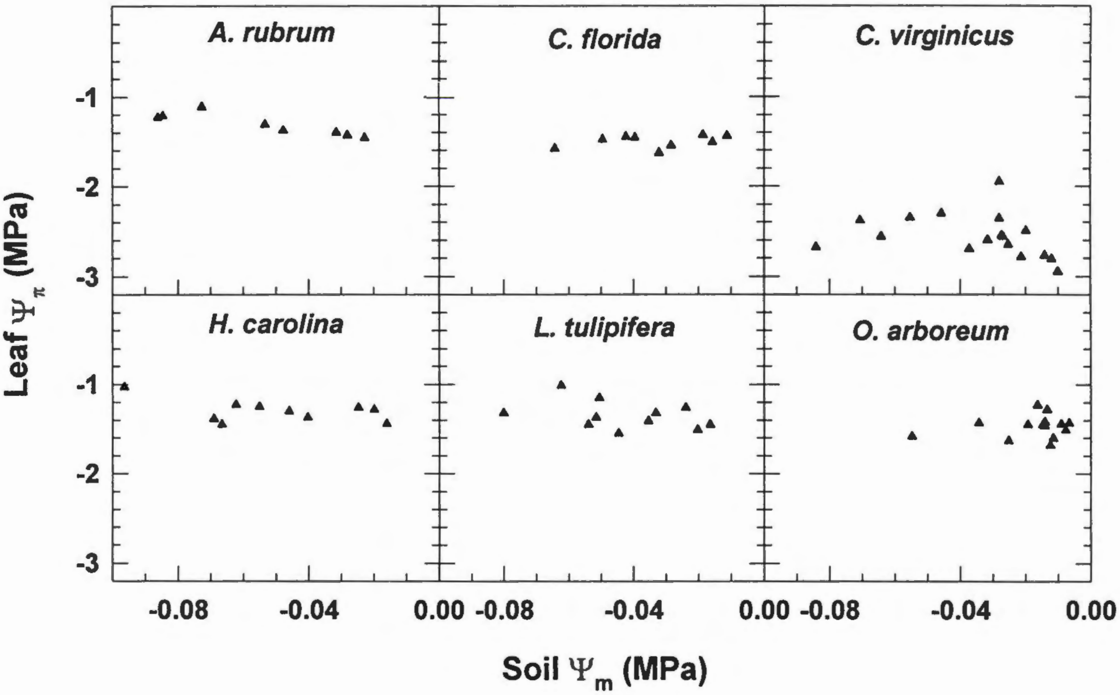


Figure 3-15. Leaf Ψ_π of WD saplings as soil Ψ_m first began to decline during the drying period. Points represent daily means for both leaf Ψ_π (n = 8) and soil Ψ_m (n=8).

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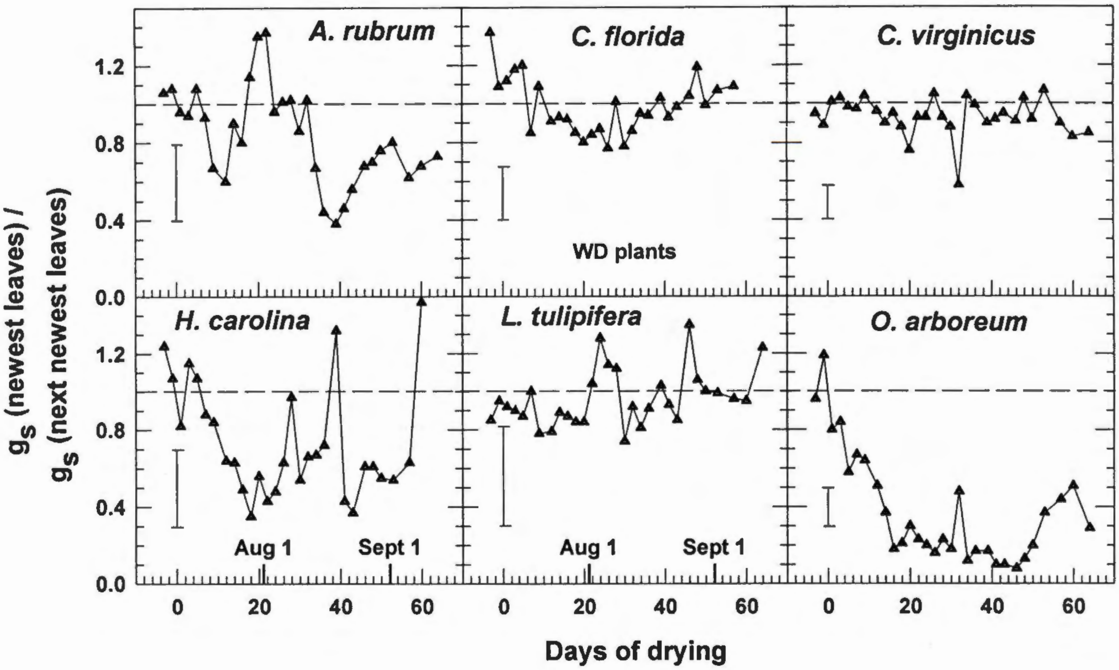

Figure 3-16. Ratio of mean stomatal conductance of the two newest leaves measured and the mean of the two next newest leaves, in half-dried plants. Points represent daily means of 8 WD replicates. Bars are standard errors of the means.

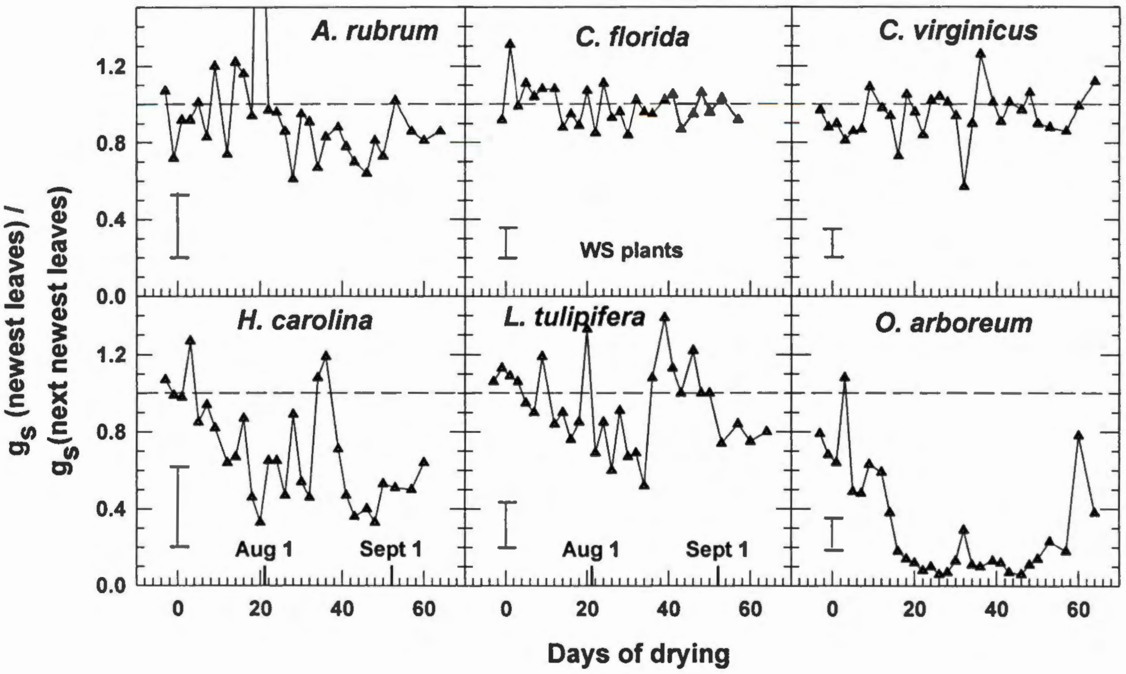

Figure 3-17. Ratio of mean stomatal conductance of the two newest leaves measured and the mean of the two next newest leaves, in half-severed plants. Points represent daily means of 4 WS replicates. Bars are standard errors of the means.

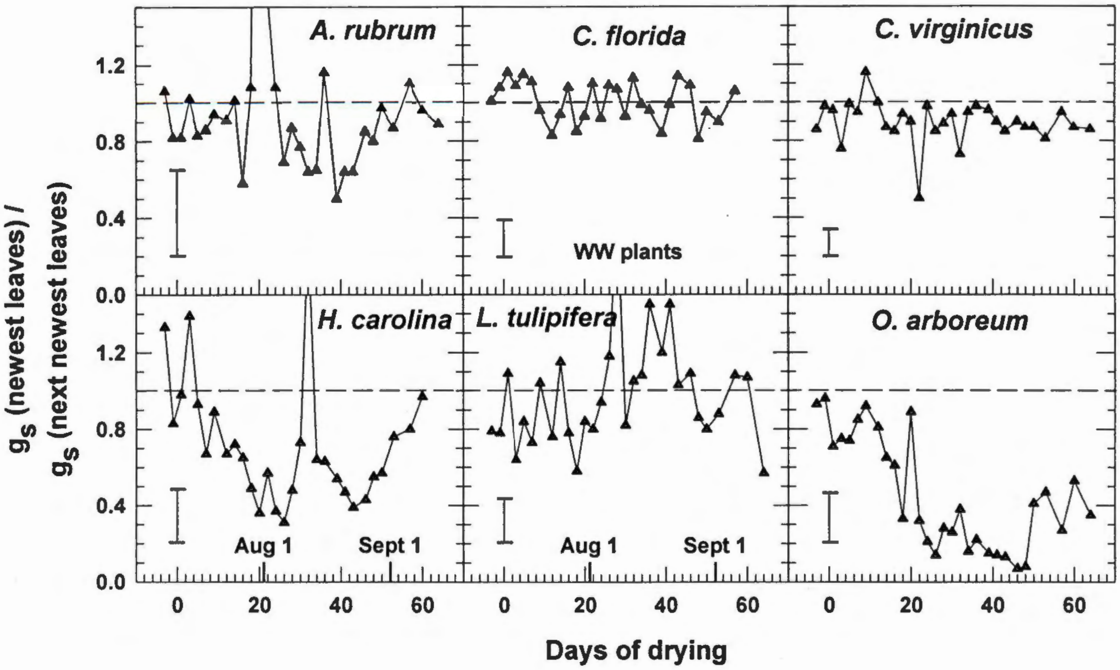

Figure 3-18. Ratio of mean stomatal conductance of the two newest leaves measured and the mean of the two next newest leaves, in fully-watered plants. Points represent daily means of 4 WW replicates. Bars are standard errors of the means.

even for these three species the g_s of newest leaves tended to be lower than the next newest leaves for the WD treatment for many days of the drying period.

Stomatal conductance of different-aged leaves responded somewhat differently to various soil Ψ_m ranges (Figures 3-19 and 3-20). Stomatal conductance of the newest leaves of *A. rubrum* was more inhibited than for the next newest leaves as soil Ψ_m dropped below -1.0 MPa. Below -1.0 MPa, relative g_s was lower for the newest leaves of all species compared to the next newest leaves, particularly for *H. carolina* and *O. arboreum*. Inhibition of g_s of the newest leaves of *H. carolina* increased as soil dried, while relative g_s of the next newest leaves was fairly constant as soil dried. Relative g_s of the newest leaves of *O. arboreum* went down quickly and remained inhibited (Figure 3-19); conversely, relative g_s of the next newest leaves increased as soil dried (Figure 3-20).

Relative g_s of the next newest leaves of *L. tulipifera* declined more rapidly than relative g_s of the newest leaves (Figures 3-21 and 3-22). Also, for *H. carolina* and *L. tulipifera*, the declines in relative g_s were better correlated with soil Ψ_m for the next newest leaves ($r = 0.86^{P \leq 0.0001}$ for *H. carolina*, $r = 0.87^{P \leq 0.0001}$ for *L. tulipifera*; Figure 3-22), compared to the newest leaves ($r = 0.74^{P \leq 0.002}$ for *H. carolina,* $r = 0.57^{P \leq 0.03}$ for *L. tulipifera*; Figure 3-21). Similarly, g_s were reduced ($P \leq 0.05$ and $P \leq 0.1$) relative to WS controls for more days for the next newest leaves for *H. carolina* and *L. tulipifera* than for the newest leaves for *H. carolina* and *L. tulipifera* (Figure 3-23 and 3-24). Conversely, for *C. florida*,

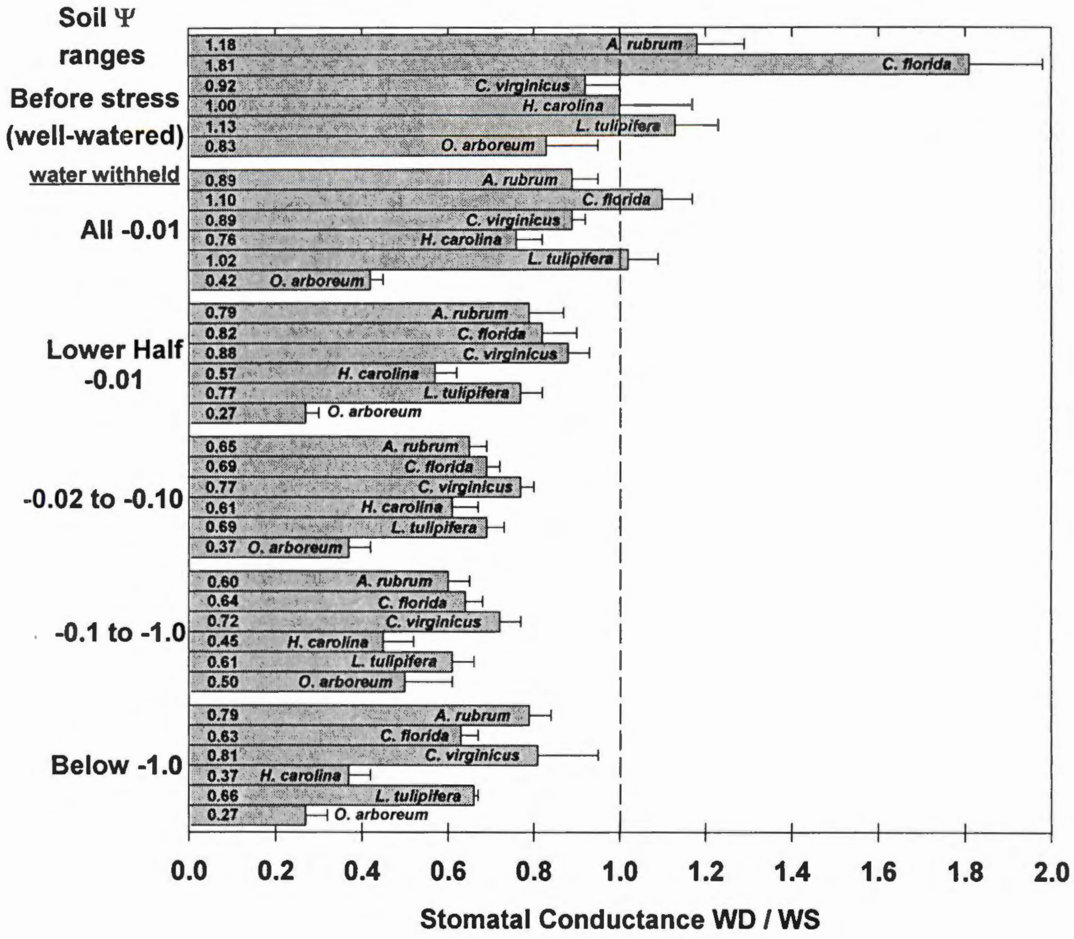

Figure 3-19. Stomatal conductance of WD saplings relative to WS controls at increasing levels of soil drying for the two newest leaves measured. Values within shaded bars are means of individual saplings for each species in a given soil Ψ_m range (n = 3 to 120). Lines above bars represent standard errors of WD means.

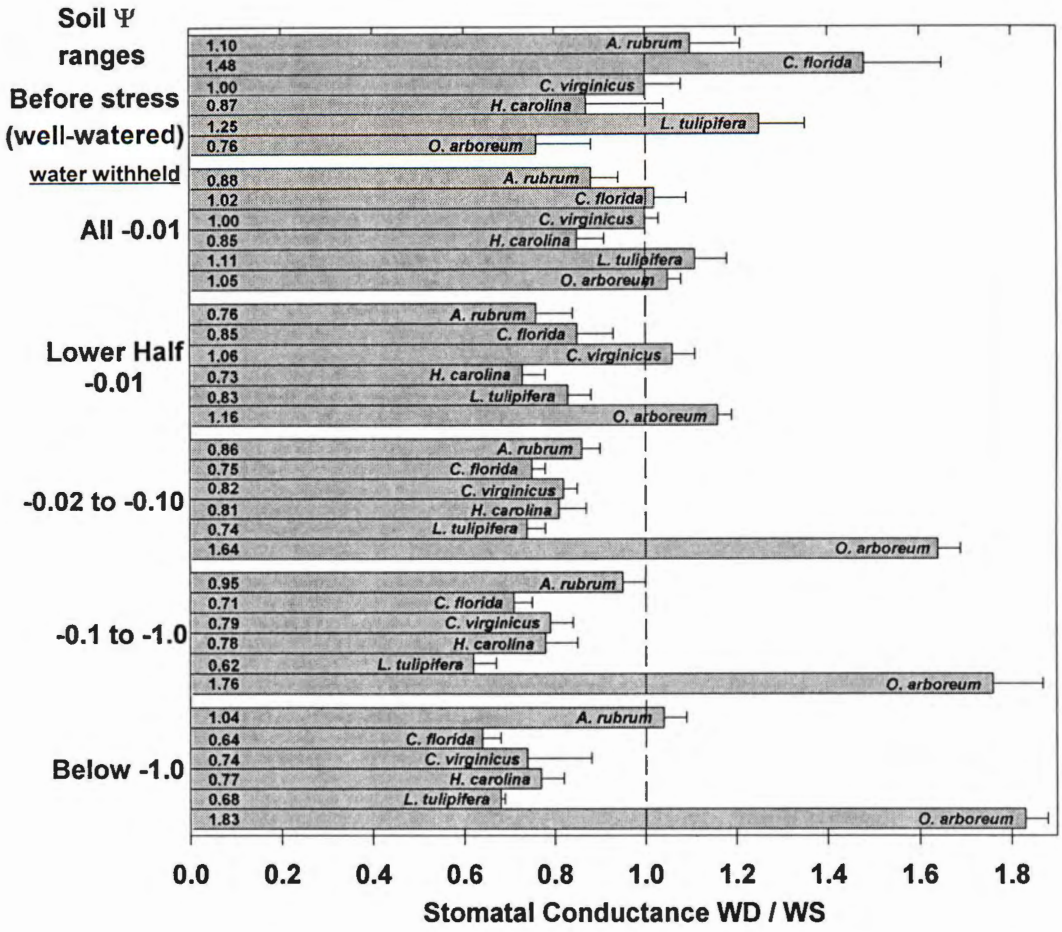

Figure 3-20. Stomatal conductance of WD saplings relative to WS controls at increasing levels of soil drying for the third and fourth newest leaves measured. Values within shaded bars are means of individual saplings for each species in a given soil Ψ_m range (n = 3 to 120). Lines above bars represent standard errors of WD means.

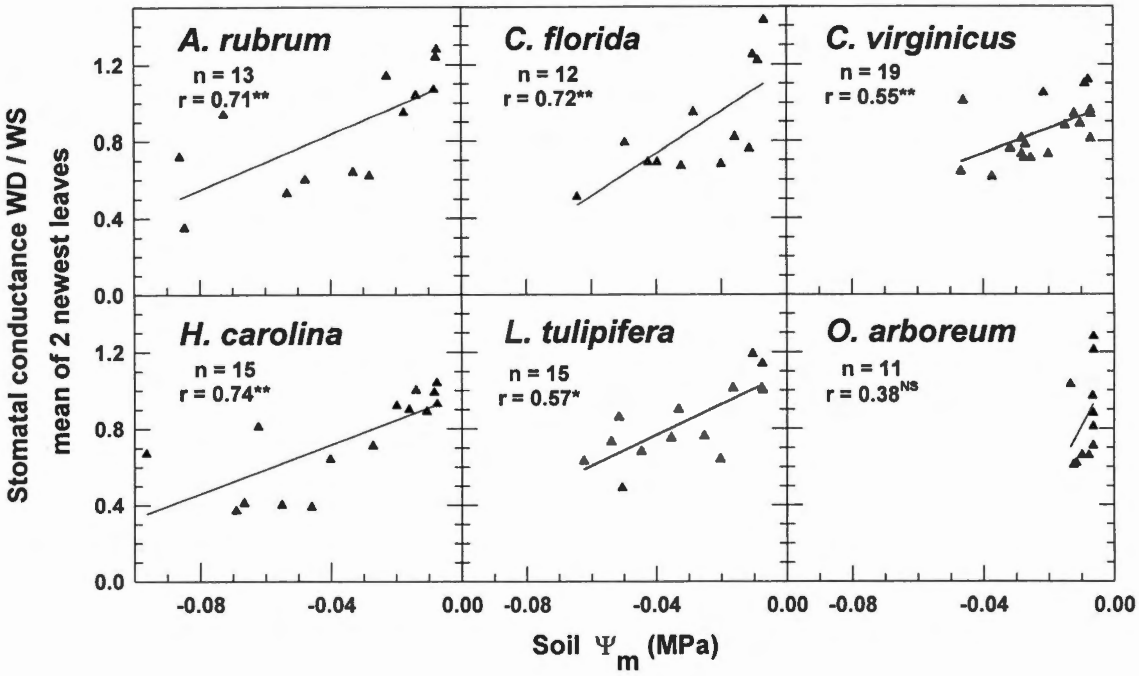

Figure 3-21. Relationship between g_s of WD as percent WS controls and soil Ψ_m for the two newest leaves measured. Points represent daily means (n = 8) and number of points regressed are indicated for each species. Symbols indicate significance of correlation (*** $P \leq 0.0001$, ** $P \leq 0.01$, * $P \leq 0.05$).

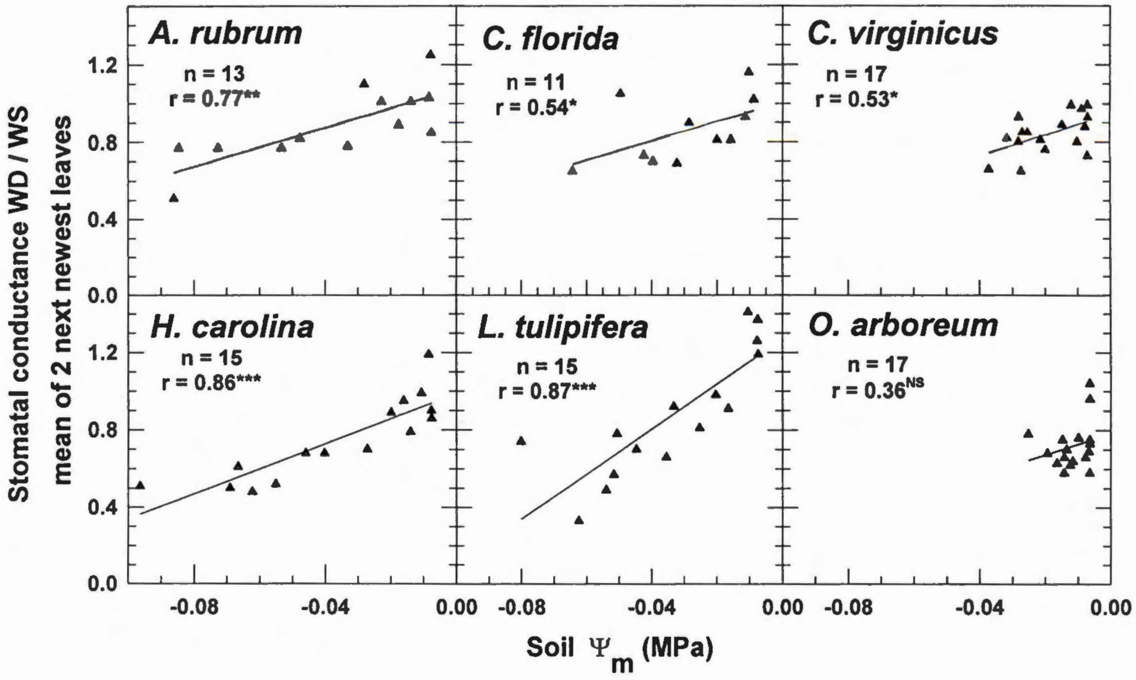

Figure 3-22. Relationship between g_s of WD as percent WS controls and soil Ψ_m for the two next newest leaves measured. Points represent daily means (n = 8) and number of points regressed are indicated for each species. Symbols indicate significance of the correlation (*** $P \leq 0.0001$, ** $P \leq 0.01$, * $P \leq 0.05$).

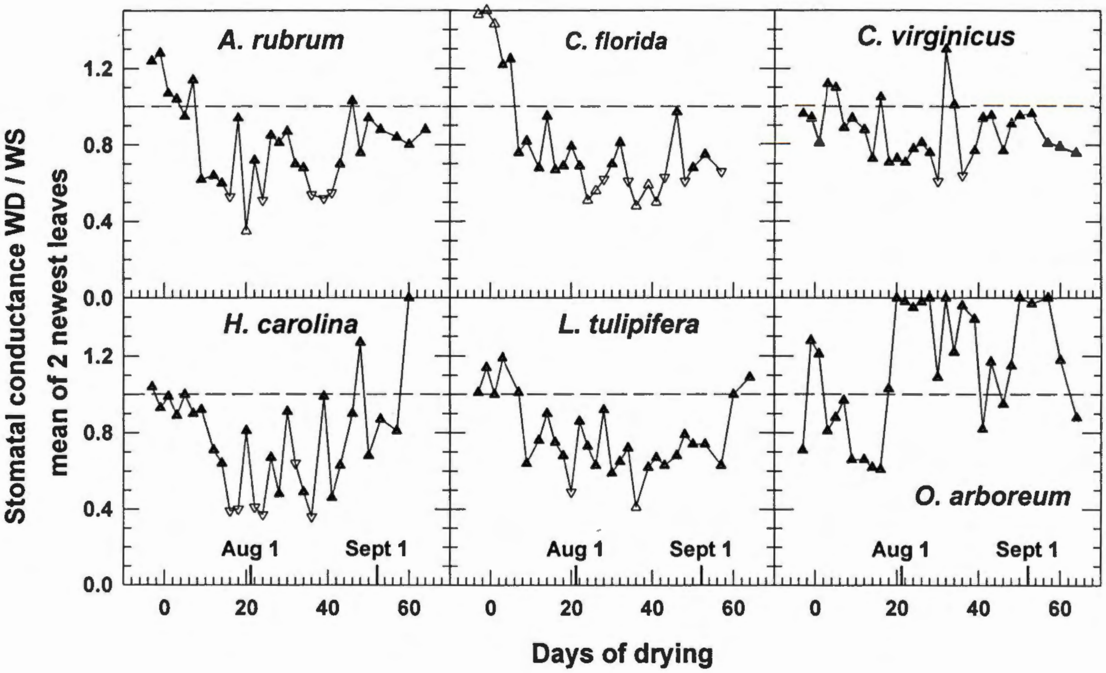

Figure 3-23. Stomatal conductance of WD saplings relative to WS controls for the mean of the two newest leaves measured. Points represent daily means (n = 8). Symbols indicate means significantly different from 100% of controls (▲ : NS, △ : $P \leq 0.05$, ▽ : $P \leq 0.1$).

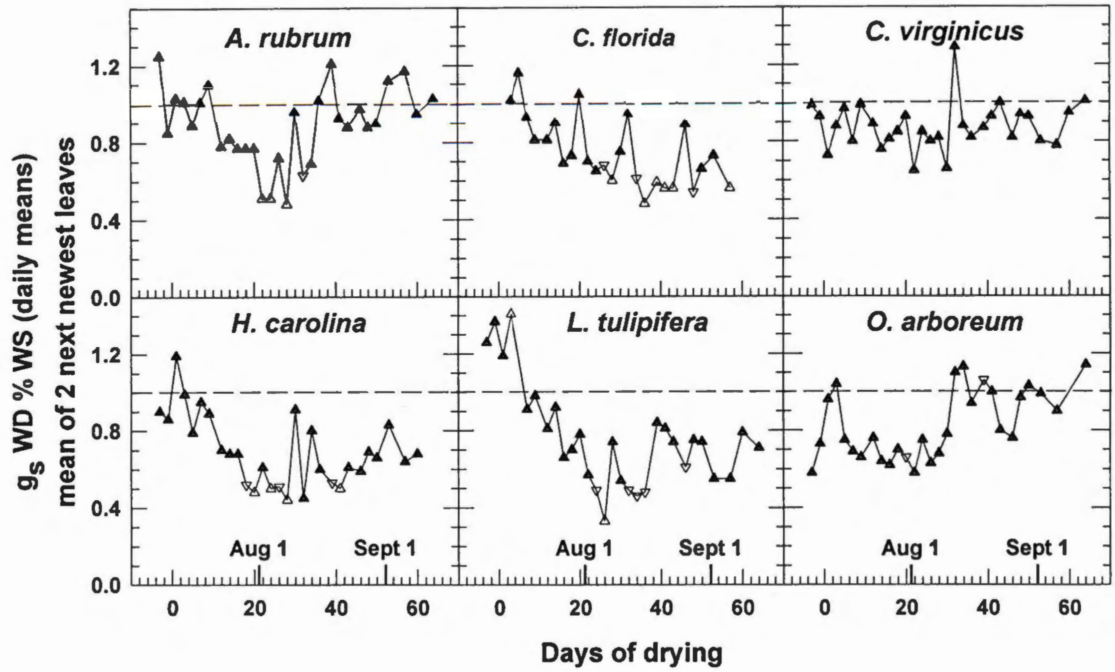

Figure 3-24. Stomatal conductance of WD saplings relative to WS controls for the mean of the two next newest leaves measured. Points represent daily means (n = 8). Symbols indicate means significantly different from 100% of controls (▲ : NS, △ : $P \leq 0.05$, ▽ : $P \leq 0.1$).

the decline in relative g_s was better correlated with soil Ψ_m for the newest leaves ($r = 0.72^{P\leq 0.008}$, Figure 3-21), compared to the next newest leaves ($r = 0.54^{P\leq 0.08}$, Figure 3-22), and g_s was reduced ($P \leq 0.05$ and $P \leq 0.1$) relative to WS controls for more days for the newest leaves than the next newest leaves for *C. florida* (Figures 3-23 and 3-24). Relative g_s were also correlated with soil Ψ_m for *A. rubrum* and *C. viginicus;* however for these species the correlation was about the same for both leaf ages (*A. rubrum*: $r = 0.71^{P\leq 0.007}$ for newest leaves, $r = 0.77^{P\leq 0.002}$ for next newest leaves; *C. virginicus*: $r = 0.55^{P\leq 0.01}$ for newest leaves, $r = 0.52^{P\leq 0.03}$ for next newest leaves). Although the correlation data do not indicate leaf age differences for *A. rubrum*, g_s was reduced ($P \leq 0.1$) relative to WS controls for more days for the newest leaves than the next newest leaves for this species. There was no correlation between relative g_s of newest or next newest leaves with declining soil Ψ_m for *O. arboreum* ($r = 0.38^{NS}$ for newest leaves and $r = 0.28^{NS}$ for next newest leaves; Figures 3-21 and 3-22), and there were few differences ($P \leq 0.1$) in relative g_s during the drying period between leaf ages (Figures 3-23 and 3-24).

4. Discussion

Stomatal inhibition occurred in tree saplings having only a portion of their roots exposed to drying soil. Since about one half of the root system was fully-watered throughout the drying period, the water status (measured here as leaf Ψ_π) of these trees was similar to that of both half-severed and fully-watered controls. The similar leaf Ψ_π across treatments suggests that the decline in g_s of half-dried plants was not the direct result of a hydraulic signal (i.e. a decline in leaf water status) but rather the result of a nonhydraulic signal. Leaf Ψ_π has been used as a reliable indicator of leaf and soil water status and is often as sensitive or a more sensitive measure of plant water status than leaf Ψ (Galladro et al. 1994). Leaf Ψ_π has been used in other studies, providing an indicator of water status that could be measured relatively quickly, reducing the possible confounding effects of temporal variations in environmental conditions (e.g. Ebel et al. 1996).

Although leaf Ψ_π was mostly consistent among treatments during the experiment, total leaf water potential Ψ can fluctuate extensively and quickly as environmental conditions change (Jones 1990b). It is possible that reductions observed in g_s of WD plants relative to WW plants could have been due to unmeasured or unmeasurable changes in leaf water status. Therefore, having only a fully-watered control would have two disadvantages: 1) our instruments were possibly not sensitive enough to measure small fluctuations in leaf water status, and 2) our measurements of water status were occasional and invasive, not continuous, thus overlooking small fluctuations. The purpose of the WS individuals was to control for possible undetected effects on leaf Ψ caused by reducing the water supply of the WD plants by half, relative to WW plants. Half-severed controls have been used in other work; for example, in a spilt-root experiment with maize, control plants with half of the root system excised and half fully-watered maintained g_s and leaf elongation rates similar to fully-watered controls with all roots intact (Saab and Sharp 1989).

Others have reported that split-root experiments are effective in determining effects of soil drying independent of alterations in leaf water relations (Blackman and Davies 1985). Wheat plants experiencing partial drying of the root system increased water absorption from other parts of the root system, indicating that a plant exposed to partial soil drying can compensate for a partial loss in water gathering capacity, thus maintaining fairly constant plant water relations (Lawlor 1973). Similarly, in maize seedlings grown in deep tubes, withholding water for 15 days exposed about 75% of total root length to soil Ψ lower than -1.1 MPa; however, the few roots remaining in wet soil supplied the plant with enough water to maintain a water supply to the shoots similar to plants in tubes watered daily (Sharp and Davies 1985).

Although nonhydraulic signaling of soil drying is now fairly well documented for some woody species, its importance in trees has been questioned (e.g. Saliendra et al. 1995). Carbon gain appears to be maximized in woody species at the expense of water loss, while water is conserved in herbaceous species at the expense of carbon gain (Knapp and Smith 1990). From this observation, one might conclude that herbaceous species would be more likely to use a nonhydraulic signal to control g_s, while it would be less likely in woody plants. Mature trees generally have relatively low photosynthetic and transpiration rates, deep and extensive root systems and large amounts of tissue for water storage. These factors may lessen the impact of water stress; therefore, the physiological status of large, mature trees may not be as dependent on environmental variation compared with small, herbaceous plants (Knapp and Smith 1990). However, due to the low boundary layer resistance, canopy transpiration of trees is expected to be regulated more by stomatal responses than herbaceous canopies which typically have much higher boundary layer resistances (Schulze 1986). As I proposed above, relative physiological homeostasis during environmental changes may be true for mature trees; however, I would expect juvenile woody plants to have physiological responses more closely tied to environmental variation, as expected with herbaceous species. Much of the work on water stress in trees has been done with seedlings and saplings (e.g. Kwon and Pallardy 1989; Abrams and Kubiske 1990). Also, younger trees controlled stomatal opening more during drying compared to older apple trees (Jones et al. 1983). Additionally, in a severe drought in a southern Appalachian hardwood forest in 1925, drought-induced damage (measured as leaf browning and early leaf senescence) was most evident among younger trees (Hursh and Haasis 1931).

Nonhydraulic signaling inhibited g_s of the saplings in this experiment. Maximum percent inhibition of g_s ranged from a low of 31% for *H. carolina* to 57% for *C. virginicus* and *O. arboreum*. These values are similar to stomatal inhibition observed in other woody species. In apple trees, the transpiration rate (controlled by stomatal opening) of half-dried plants was reduced down to 30% of controls (Gowing et al. 1990). Similarly, half-dried sycamore trees exhibited reductions in g_s down to 26% of control seedlings (Khalil and Grace 1993).

Not only was g_s inhibited by a nonhydraulic, root-sourced signal in woody saplings, but also the maximum amount of inhibition observed for the woody plants appeared to be larger than the extent of inhibition documented in many herbaceous plants. Stomatal conductance was reduced relative to controls in half-dried cowpea (down to 70%; Ebel et al. 1996), sorghum (down to 65% of controls; Augé et al. 1995), mycorrhizal maize (76% of controls) and nonmycorrhizal maize (down to 60% of controls; Augé et al. 1994). In other work with maize, nonhydraulic signaling resulted in 50% or larger declines in g_s compared to controls, similar to some of the species in this study (Blackman and Davies 1985; Zhang and Davies 1989, 1990b). Similarly, g_s in rice was reduced up to 50% by nonhydraulic signaling (Bano et al. 1993).

Our results support the hypothesis for a positive nonhydraulic signal because there was little difference between conductances of WS and WW controls. If the signal were a negative signal (such as a reduced supply of cytokinins, Blackman and Davies 1985; Davies et al. 1986), the g_s of WS plants would have been reduced relative to the WW controls as observed with the WD saplings, since their water supply was also reduced by about half.

The nonhydraulic signal is likely an increased production of ABA in root tips (e.g. Zhang and Davies 1987). Jones (1990a) argues that ABA would not be a likely candidate for a root signal because it is produced in drying root tips which are therefore not contributing to the transpiration stream; however, we observed stomatal closure relatively high soil Ψ_m (> -0.1 MPa) indicating that signaling may have occurred before Ψ of the half-dried roots became too low to contribute to the plant's water supply. Similarly, maize roots in soil Ψ higher than -0.5 MPa were much more effective in supplying water to the shoot than roots in drier soil (i.e. roots at soil Ψ of -0.5 MPa or lower had slower soil water depletion rates, Sharp and Davies 1985).

As soil continued to dry, g_s for *C. florida, C. virginicus* and *L. tulipifera* remained inhibited while g_s for A*. rubrum, H. carolina* and *O. arboreum* increased (though g_s values were still lower than WS controls on most days). For *C. florida, C. virginicus* and *L. tulipifera,* the continued inhibition may have continued to move from very dry roots to shoots or stomata may have not recovered quickly, even after the signal diminished. For the other three species, the increase observed may have been due to a reduced loading of root xylem and/or root-to-shoot transport of the nonhydraulic signal (possibly ABA) once soil drying became more severe. A similar initial decline in g_s, followed by an increase as soil dried further, has also been observed in sycamore seedlings (Khalil and Grace 1993). In wheat, stomates closed after initial exposure to ABA, then stomates recovered, indicating that a continual supply of ABA may be needed to maintain reduced g_s (Atkinson et al. 1989). In a split-root system, the roots in fully-watered soil will continue to grow while the roots in dry soil would not be expected to grow as much and may possibly even die as soil drying becomes severe. Thus, the effect of the split-root system treatment (i.e. half of roots in drying soil resulting in production of a nonhydraulic signal) may be expected to decline as root growth in the wet pot exceeds growth in the dry pot (Davies et al. 1986).

Soil Ψ_m increased near the end of the experiment for some individuals of *A. rubrum, C. florida, H. carolina, L. tulipifera* and *O. arboreum.* The most likely explanation of this occurrence is that the roots in drying soil were rehydrated by the roots in wet soil. Although reverse transport of water from roots to soil has been disputed (e.g. Kirkham 1980; Molz and Peterson 1976), rehydration of roots in drying soil has been observed by several others in split-root experiments (e.g. cowpea, Ebel et al. 1996; maize, Augé et al. 1994, Saab and Sharp 1989; and sorghum, Ebel et al. 1994, Xu and Bland 1993).

Stomatal inhibition was first observed at fairly high soil Ψ_m. Soil Ψ_m above -0.1 MPa initiated stomatal inhibition of 20% or more in all species. Soil Ψ_m ultimately reached -3 MPa or lower in all species, excluding *C. virginicus* and *O. arboreum*. Individuals of these two species were smaller, had less foliage, and lower root dry weights which explains why they did not dry the soil as quickly or to as large an extent as the other four species. There was also much variation among individual plants in drying rates, explaining why soil Ψ_m was not detected as significantly different from fully-watered soil until later in the drying period. A small decline in root Ψ can initiate a nonhydraulic signal in maize (Saab and Sharp 1989). Some herbaceous species seem less sensitive to soil drying. In sunflower (Gollan et al. 1986, 1992) and wheat (Gollan et al. 1986; Passioura 1988), g_s of plants in drying soil was not inhibited until soil Ψ reached about -0.3 MPa, lower than the soil Ψ_m levels at 80% stomatal inhibition we observed in tree species.

L. tulipifera, *A. rubrum, O. arboreum* and *H. carolina,* all cove hardwoods often found in moist, bottomland habitats, were determined to have relatively dehydration sensitive leaf tissues (i.e. high lethal leaf Ψ, Augé et al. unpublished). In a previous study, *A. rubrum* was found to be one of the most sensitive among six woody species, showing rapid stomatal closure at relatively high leaf Ψ (Davies and Kozlowski 1977). Also, stomates of *L. tulipifera* were found to be sensitive to a variety of environmental stresses, including drought

(Roberts 1990). We proposed that as drought avoiders, these species would respond most quickly to and to the largest extent to nonhydraulic signaling, as has been observed with some herbaceous species (e.g. cowpea, Ebel et al. 1996). However, *L. tulipifera* and *A. rubrum* both required the most soil drying to inhibit g_s to 80% of WS controls and their maximum inhibition was intermediate among species. *A. rubrum* and *L. tulipifera* may rely more on mechanisms other than nonhydraulic signaling to avoid drought, such as deep rooting or changes in leaf morphology. Maybe these two species have not developed many avoidance mechanisms and that is why they are typically found on moist sites and are less productive on more xeric sites. For example, it has been predicted that *Acer* species would be limited to moist sites and may be poor competitors on drier sites (Davies and Kozlowski 1977). Also, *L. tulipifera* may be found on side slopes and ridge tops in East Tennessee and in other eastern forests, but these trees are generally not as large as mesic site trees (Abrams 1994; Luxmore et al. 1978).

Soil Ψ_m required to initiate nonhydraulic inhibition of g_s was highest for *O. arboreum and C. virginicus*, indicating that these species may be relatively more sensitive to nonhydraulic signaling of soil drying. This observation is consistent for *O. arboreum* with previous water-stress work. As noted above, *O. arboreum* is considered a mesic site tree and has been found to be fairly dehydration sensitive (Augé et al. unpublished). Also, leaf browning in a severe drought in

1925 was particularly severe for *O. arboreum* and *C. florida* (Hursh and Haasis 1931). Despite this apparent sensitivity, *O. arboreum* and *C. virginicus* had the least extensive inhibition overall, which may suggest that they are less sensitive to nonhydraulic signaling of soil drying. It is possible, however, that larger maximum inhibition values would have been observed for *O. Arboreum* had it dried soil as extensively as other species.

In a study of several deciduous tree species during a drought period (e.g. *Acer saccharum, Juglans* spp., *Quercus* spp.), *C. florida* was the first to show stomatal inhibition and stomates were closed for the highest percentage of days during the growing season among species (Hinckley et al. 1979). Others have also found that *C. florida* is usually not very tolerant to drought (Bahari et al. 1985); however, this species has a relatively low lethal leaf Ψ indicating that it may not have well-developed drought avoidance mechanisms (Augé et al. unpublished). *C. florida* is known to be a shallow-rooted tree in natural settings (Kramer 1989). *C. florida* was one of the more sensitive species to nonhydraulic signaling, but stomates did not recover near the end of the experiment as observed for some of the other species.

C. virginicus was determined to be relatively dehydration tolerant among several deciduous tree species (Augé et al. unpublished); however, across a broader spectrum of plants, its lethal Ψ defines it as intermediate in dehydration tolerance reported for several different species (Ludlow 1989). Even though *C.*

viginicus is relatively dehydration tolerant its stomates responded fairly quickly to nonhydraulic signaling of soil drying. This species has also been found to osmotically adjust during drought, which may be why its nonhydraulic inhibition of g_s was the least extensive observed among the species we examined.

In a study of several deciduous tree species, those determined to be early successional species had smaller reductions in gas exchange compared to later successional species in this study, *C. florida* and *A. rubrum* (Abrams and Mostoller 1995). Early and mid-successional species also had higher drought tolerance than late successional species. This agrees with our determination of *C. florida* and *A. rubrum* as relative drought avoiders (Augé et al. unpublished).

Stomatal inhibition during the drying period was higher in the younger than in older leaves of *H. carolina* and *O. arboreum*, and *A. rubrum*. Stomatal inhibition did not vary much with leaf age in *L. tulipifera, C. virginicus* and *C. florida* during the drying period. In several herbaceous species, the youngest leaves of drought- stressed plants have been observed to have higher ABA levels and larger declines in g_s compared with older leaves (e.g. wheat, Atkinson et al. 1989; *Lupin*, Correia and Pereira 1995; *Xanthium,* Raschke and Zeevaart (1976); and *Ricinus* and *Xanthium*, Zeevaart and Boyer 1984). Conversely, g_s of cotton in water-stressed plants was reduced more for older leaves compared to youngest leaves, although the measured ABA accumulations were negatively related to the reduction in g_s (i.e. ABA concentration was higher in youngest leaves; Ackerson 1980, Jordon et al. 1975).

Maximum leaf conductance probably does not change much in leaves of deciduous hardwoods during the period between complete leaf maturation and initial senescence (Hinckley and Teskey 1981); however, maximum leaf conductances do vary in developing foliage. For example, immature *Quercus alba* leaves had relatively high cuticular conductances due presumably to incomplete development of the stomatal mechanism and vascular elements in ring porous species (Hinckley and Teskey 1981). The youngest leaves we measured were fully expanded, mature leaves. Most evidence indicates that g_s is fairly constant with leaf age except for senescing leaves and the most immature leaves (e.g. Hinckley and Teskey 1981). More work is needed to clarify the different effects of nonhydraulic signaling due to leaf age.

In conclusion, nonhydraulic signaling did result in stomatal inhibition in saplings exposed to partial soil drying. The extent of inhibition observed was similar to previously reported values for other woody species and was larger than much of the inhibition reported for several herbaceous species. Very little soil drying was required to initiate stomatal closure. Species varied in sensitivity of stomatal opening and extent of stomatal inhibition due to nonhydraulic signaling, as was expected based on the native habitats of the species studied. Also, stomatal inhibition varied with leaf age in some species but not in others. Comparison of nonhydraulic signaling characteristics with previously determined relative drought resistance profiles indicated that the nonhydraulic signaling mechanism was probably not allied with other drought strategies of species classified as drought avoiders.

Precipitation records show much annual and seasonal fluctuation for the southern Appalachian region. Periodic, severe droughts, such as the episode recorded in this region in 1925 (Hursh and Haasis 1931), may become more common as global temperatures increase and precipitation patterns change. Research on the drought resistance profiles of deciduous trees will be useful in predicting tree species distribution and will be economically valuable for the forestry industry in selecting species and genotypes best suited for planting on drought prone sites (Pallardy 1981).

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